Recent Species of the Genus *Petricola* in the Eastern Pacific (Bivalvia: Veneroidea)

by

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Abstract. The taxonomy of 16 Recent eastern Pacific species that have been allocated to the bivalve genus Petricola is discussed. Two new species, Petricola hertzana and P. scotti are described. Fifteen lectotype designations are made. One species is placed in the genus Choristodon, two in the genus Petricolaria, four species in Petricola (Petricola), and five in Petricola (Petricolirus); four species remain in Petricola, s.l. A list is provided of species-level taxa excluded from the family (and nomina dubia).

INTRODUCTION

About 2 years ago, during preparation of a volume on the bivalves of the northeastern Pacific (Coan et al., in preparation), I noted several nomenclatural problems involving eastern Pacific species that have been allocated to the bivalve genus *Petricola*. The present study addresses these problems. There is by no means a consensus on the arrangement of the genera within the Petricolidae, or even which genera are members of that family, or indeed on the arrangement of the families and subfamilies in the Veneroida as a whole. I hope that improving the understanding of the eastern Pacific petricolids will be useful to workers addressing these broader topics.

This group was more difficult to understand than I anticipated. In part, this is because unlike the California *Petricola (Petricola) carditoides* (Conrad, 1837), one of the most common marine bivalves on the West Coast with an extremely variable morphology depending on its nestling site, many other taxa seem to be very uncommon, making it difficult to understand the limits of their variability. A second reason for the difficulty in working out the eastern Pacific species is the high proportion of missing type material, compounded by early, cryptic descriptions unaccompanied by illustrations.

Key treatments on the systematics of the Petricolidae

in general are those of Deshayes (1853, 1855), G. B. Sowerby II (1854b, 1874a), Tryon (1872), Dall (1900c), Jukes-Browne (1910), Lamy (1921, 1923b), Habe (1951, 1951–1952, 1977), and Keen (1969). A short account of the present study has appeared in a newsletter (Coan, 1996).

FORMAT

In the following treatment, each valid taxon is followed by a synonymy, information on type specimens and type localities, notes on distribution and habitat, and an additional discussion.

The synonymies include all major accounts about the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes given in brackets.

The distributional information is based on specimens I have examined, except as noted. For many species, the available habitat information is sparse. I have summarized the data available. Most occurrences in the fossil record are taken from the literature.

References are provided in the Literature Cited for all works and taxa mentioned.

The following abbreviations for institutions and collections are used in the text: AMNH, American Museum of Natural History, New York, New York, USA; ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; BM(NH), British Museum (Natural History)

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collection in The Natural History Museum, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; LACM, Natural History Museum of Los Angeles County, California, USA; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MHNG, Muséum d'Histoire Naturelle, Geneva, Switzerland; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNH-U, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; PRI, Paleontological Research Institution, Ithaca, New York, USA; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA; SDNHM, San Diego Natural History Museum, San Diego, California, USA; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, United States National Museum collection, National Museum Natural History, Smithsonian Institution, Washington, DC, USA; PMYU, Peabody Museum, Yale University, New Haven, Connecticut, USA: UMML, University of Miami Marine Laboratory [Rosensteil School of Marine and Atmospheric Sciences], Miami, Florida, USA; ZISP, Zoologischeskii Institut, St. Petersburg, Russia; Hertz Collection, collection of Carol and Jules Hertz, San Diego, California USA; Redfern Collection, collection of Colin Redfern of Boca Raton, Florida, USA; Skoglund Collection, collection of Carol C. Skoglund, Phoenix, Arizona, USA.

DIFFERENTIATING CHARACTERS

Shape: Many species have a characteristic shape. For example, *Petricolaria cognata*, which penetrates soft substrata, is always elongate (Figures 49, 50, 69), and *Choristodon robustum*, which inhabits and can enlarge cavities in coral and other calcareous substrata, is always ovate (Figures 42–48, 68). However, other species, such as *Petricola carditoides*, which nestles in existing cavities and has only limited capacity to enlarge its home, can vary enormously in shape (Figures 3–12). I have here given the most characteristic shape, including the relative position and prominence of the beaks, degree of inflation, shell thickness, and prominence of the beaks, while noting the potential for variability.

The term **ovate** means a length/height ratio of 1.0 to 1.5; **ovate-elongate**, a l/h ratio of 1.5 to 2.0; **elongate**, a l/h ratio of 2.0 to 3.0; **very elongate**, a l/h ratio of greater than 3.0. **Anterior end shortest** means that the anterior end is from 40% to 30% of shell length; **anterior end short**, from 30% to 20%; **anterior end very short**, less than 20%. The term **inflated** means having a thickness/height ratio of 0.5 to 1.0; adult specimens of only two taxa may be **flattened**, with a ratio of less than 0.5.

Sculpture: As with many bivalves, the external sculpture is often diagnostic. Radial sculpture predominates in most members of the Petricolidae, and may be characterized

by the number of ribs and where the most prominent ribs occur. Commarginal elements may also be present, from mere growth checks to conspicious lamellae.

Pallial sinus/pallial line: The shape of the pallial sinus is an important differentiating character, particularly its depth, whether it is rounded or pointed anteriorly, and the extent to which it is horizontal or is directed dorsally. The pallial sinuses of most species are of moderate depth, being from about 50% to 60% of the shell length (Figures 55, 56, 58, 60–68, 70); deep sinuses are greater than 60% of shell length (Figures 57, 59, 69); in some specimens of one species, the sinus may be shallow and close to 40%. The pallial sinuses of some taxa are pointed anteriorly (Figures 61, 69, 70), but most are rounded. A broad pallial sinus has a ratio between the vertical dimension at its posterior end to its length of from 2.5 to 1.1; a moderate sinus of 1.0 to 0.8; a narrow sinus of 0.7 to 0.3. The pallial line anteroventral to the pallial sinus is also important, being slightly confluent (Figures 56, 64, 65, 67), substantially confluent (Figures 57, 66), closely paralleling (Figure 59) or entirely separate from the sinus (Figures 60-63), and it may be bowed dorsally to a greater (Figures 57, 64-66) or lesser (Figures 59, 67) extent.

Hinge: Whereas nearly all the species treated have two cardinal teeth in the right valve and three in the left, the anterior cardinal in the left valve may disappear in the adult, or be absent entirely. The hinge and teeth vary in robustness and in such details as their length and which of them are bifid. Two species have a low posterior lateral-ridge in the right valve.

Ligament: The ligament on all species is external, but a portion of it may be sunken onto the hinge, and this is particularly important in differentiating the species. A partly sunken ligament occurs in members of *Petricola* (*Petricola*) (Figures 55–58) and in *Choristodon* (Figure 68); in the rest, it is not sunken.

Color: Although many species are drab, being white or tinged with brown, in some cases color pattern can provide important clues, and overall color is characteristic of two species.

Lunule/escutcheon: Most species have neither, but each puts in a token appearance among these taxa.

SYSTEMATIC ACCOUNT

Family PETRICOLIDAE d'Orbigny, 1840

[Deshayes, 1830:Table on classification of the bivalves, as Family "Pétricolées," but not

accepted as of this date by later authors; dated as first Latinized by d'Orbigny, 1840:109; ICZN

Code Art. 11f(iii)]

Genus Petricola Lamarck, 1801

Petricola Lamarck, 1801:121 [Type species: Petricola costata Lamarck, 1801:121, = Venus lapicida Gmelin, 1791:3269, which is based on Chemnitz, 1788: 356– 357, pl. 172, figs. 1664, 1665; subsequent designation of Schmidt, 1818:55, 176]. Recent, western Atlantic, IndoPacific.

- Naranio Gray, 1853:38 [Type species: Petricola costata Lamarck, 1801, = Venus lapicida Gmelin, 1791; subsequent designation of Lamy, 1923b:318].
- Pseudoirus Habe, 1951:98; 1952:187 [Type species (original designation): "Petricola mirabilis Deshayes, 1853," auctt., non Deshayes, 1853]. Recent, Japan. (See Discussion under Petricola carditoides.)

Members of this genus are ovate to elongate, with fine to heavy radial sculpture; sculpture divaricate or zig-zag in some taxa. Ligament superficial to partially sunken below hinge margin.

Up to the 1940s, when Winckworth (1944:24) pointed out Schmidt's (1818) type designation for the genus *Petricola*, the type species was generally taken to be *Venus lithophaga* Retzius, 1788. As a result, Gray (1853) established the genus *Naranio* for *Petricola costata*, and *Rupellaria* Fleuriau de Bellevue, 1802, of which *Venus lithophaga*, is the type species, was considered to be a synonym of *Petricola*.

No original specimen from the Chemnitz material that formed the basis of Gmelin's *Venus lapicida* is now present in the Universitetets Zoologisk Museum in Copenhagen (T. Schiøtte, e-mail, 22 May 1995), but there is little doubt as to its identity.

Habe's genus *Pseudoirus* was established for a Japanese species identified as "*Petricola mirabilis* Deshayes, 1853," chiefly on the basis that it does not occur in coral. The sculpture is otherwise similar. Until more is known about its morphology, *Pseudoirus* should be regarded as a synonym of *Petricola*, *s.s.* If the genus proves to be needed, this can be interpreted as case of a "misidentified type species" (ICZN *Code* Art. 70b), requiring a petition to the International Commission on Zoological Nomenclature to resolve.

Subdivision of this genus into meaningful subgenera or genera awaits more detailed morphological studies by other workers. Four eastern Pacific species are associated with *Petricola*, *s.s.* Five other species are tentatively placed in the subgenus *Petricolirus*, while four species remain in *Petricola*, *s.l.*

Subgenus Petricola Lamarck, 1801, sensu stricto

Members of this subgenus have fine, divaricating, sometimes zig-zag sculpture, an ovate shape, and a some-

what sunken ligament. At least the type species is thought to be able to use chemical secretions as an aid in enlarging its burrows in calcareous substrata.

Petricola (Petricola) botula Olsson, 1961

(Figures 1, 2, 55)

Petricola (Naranio) botula Olsson, 1961. Olsson, 1961:317, pl. 55, figs. 7, 7a [mislabeled as 1, 1b in plate explanation], 8; Keen, 1971:197 [as a possible synonym of *P. exarata*]; Bernard, 1983:57 [as a synonym of *P. exarata*].

Type material & locality: *P. botula* ANSP 218908, left valve; length, 14.4 mm; height, 7.9 mm; thickness, 3.6 mm (Figure 1). Judging by the originally listed measurements, there were at least four paratypes (15.5 mm, 13.7 mm, 12.5 mm, 11.4 mm), but none of these are in the ANSP, as indicated by Olsson (1961), nor are they at the PRI or the UMML. However, the latter does have three paratypes (UMML 30.9601) of lengths 9.9 mm (right valve), 7.8 mm (right valve), and 7.6 mm (pair). [Punta] Guánico, Península de Azuero, Los Santos Province, Panamá (7.3°N).

Description: Shell ovate to ovate-elongate; anterior end short, rounded; posterior end rounded. Shell inflated, moderately heavy; beaks inflated. Without lunule or escutcheon. Sculpture of 90-100 very fine radial ribs that bifurcate in various places over entire surface. Pallial sinus of moderate depth, broad, not projecting dorsally, rounded, paralleling or confluent with pallial line for a very short distance; pallial line not significantly bowed dorsally (Figure 55). Hinge moderately heavy; right valve with a triangular anterior cardinal and a bifid posterior cardinal; left valve with a small anterior cardinal, a conspicuously bifid central cardinal (broad in the two northern lots), and an elongate posterior cardinal. Ligament of moderate length, deeply sunken; nymph heavy. Color white within and without. Length to 15.5 mm (a paratype listed by Olsson, 1961). A specimen from Mexico is also illustrated here (Figure 2).

Geographic distribution and habitat: Mazatlán, Sinaloa (23.3°N) [SBMNH 128884]; Tizate, Bahía Banderas, Nayarit (20.8°N) [Skoglund Collection] (Figure 2), Mexico, to Punta Guánico (7.3°N) [type locality] and Bahía Chame (8.6°N) [UMML 30,9602], Los Santos Province,

Explanation of Figures 1 to 7

Figures 1, 2. Petricola (Petricola) botula Olsson, 1961. Figure 1. Holotype; ANSP 218908; length, 14.4 mm. Figure 2. SBMNH 143211; Tizate, Bahía Banderas, Nayarit, Mexico; length, 15.0 mm. Figures 3–7. Petricola (Petricola) carditoides (Conrad, 1837). Figure 3. Saxicava carditoides; original figure; length, 38 mm. Figure 4. S. californica Conrad, 1837; original figure; length, 27 mm. Figure 5. S. legumen Deshayes, 1839; original figure; length, 37 mm. Figure 6. Petricola arcuata Deshayes, 1839; holotype; MNHN; length 38.2 mm. Figure 7. P. cylindracea Deshayes, 1839; original figure; length, 20 mm.



Table 1

Relative frequency in collections: number of lots studied.

Petricola carditoides	516
Petricola californiensis	251
Petricola denticulata	181
Petricolaria cognata	91
Choristodon robustum	82*
Petricola lucasana	73
Petricola hertzana	55
Petricola rugosa	37
Petricola exarata	34
Petricola dactylus	32
Petricolaria pholadiformis	32*
Petricola linguafelis	23
Petricola olssoni	22
Petricola s cotti	9
Petricola concinna	8
Petricola botula	5
Total lots examined	1,451

* Eastern Pacific lots only.

Panamá, boring into rock or clay. I have examined five lots.

Discussion: This species is very poorly known. With its bifurcating sculpture and deeply sunken ligament, it most closely resembles *P. lucasana*, from which it differs in being more inflated, in having finer, more even sculpture and a less sunker ligament, and in lacking red coloration. The right valve also lacks the posterior lateral ridge present in *P. lucasana*. It differs from *P. carditoides* in having coarser sculpture.

Petricola (Petricola) carditoides (Conrad, 1837)

(Figures 3-12, 56)

Saxicava carditoides Conrad, 1837. Conrad, 1837:255–256, pl. 20, fig. 8; [all the following as *Petricola*]; Conrad, 1849b:213; Carpenter, 1857a:214 [as a synonym of *P. californica*]; Carpenter, 1857b:196, 229, 232, 234, 284; Carpenter, 1864b:526, 528, 534, 536, 540, 590, 592, 602, 634, 641 [1872:12, 14, 20, 22, 26, 76, 78, 88, 120, 127] [with *P. californica* as both a junior or senior synonym]; Tryon, 1872:255, 257 [as a synonym of *P. nivea* "(Chemnitz, 1785)"]; Arnold, 1903:154 [*Petricola* (*Petricola*]]; Dall, 1921:44; Lamy, 1923b:334–337; I. S. Oldroyd, 1924:50, 214, pl. 42, fig. 6a, b; I. S. Oldroyd,

1925:163, pl. 34, fig. 6a, b; Grant & Gale, 1931:355, 906, pl. 13, figs. 14a, b; Burch, 1944:19 [*Petricola (Rupellaria)*]; Keen, 1966a:170; Addicott, 1966:4, pl. 4, figs. 2, 3; Hertlein & Grant, 1972:283–284, pl. 44, figs. 15, 16 [as *Petricola (Rupellaria)*]; Bernard, 1983:57 [*Petricola (Rupellaria)*].

- Saxicava californica Conrad, 1837. Conrad, 1837:256, pl. 20, fig. 9; [the following all as *Petricola*]; Conrad, 1849b:213; Deshayes, 1853:208; Carpenter, 1857a:214; Carpenter, 1857b:196, 229, 299, 349, 351; Carpenter, 1864b:526, 559, 634, 641 [1872:12, 45, 120, 127] [as a junior synonym of *P. carditoides*]; Tryon, 1872:255, 257 [as a synonym of *P. nivea*]; Arnold, 1903:154 [as a synonym of *P. carditoides*]; Lamy, 1923b:334 [as a variety of *P. carditoides*]; Keen, 1966a:170 [as a synonym of *P. carditoides*]; Bernard, 1983:57 [as a synonym of *P. carditoides*].
- Saxicava legumen Deshayes, 1839. Deshayes, 1839:358;
 Deshayes, 1841:1–2, pl. 29; Carpenter, 1857b:202, 203
 [as a synonym of *Hiatella pholadis* (Linnaeus, 1771)];
 Carpenter, 1864b:528, 529, 637 [1872:14, 15, 123] [as a synonym of *Hiatella pholadis*]; Dall, 1898:835 [as a possible synonym of *P. carditoides*]; Grant & Gale, 1931:355 [as a possible synonym of *P. carditoides*]; Bernard, 1983:59 [as a synonym of *Hiatella pholadis*].
- Petricola arcuata Deshayes, 1839. Deshayes, 1839:358; Deshayes, 1840:2–3, pl. 19; [the following four references as a synonym of *P. californica*]; Conrad, 1849b:213; Deshayes, 1853:208; Carpenter, 1857a:214; Carpenter, 1857b:196, 203, 229; Carpenter, 1864b:526, 528, 559, 634, 641 [1872:12, 14, 45, 120, 127] [as a synonym of *P. carditoides*]; Tryon, 1872:255, 257 [as a synonym of *P. nivea*]; Lamy, 1923b:334 [as a synonym of *P. carditoides*]; Arnold, 1903:154 [as a synonym of *P. carditoides*]; Bernard, 1983:57 [as a synonym of *P. carditoides*].
- Petricola cylindracea Deshayes, 1839. Deshayes, 1839:358–359; Deshayes, 1840:3–4, pl. 20; Conrad, 1849b:213 [as a possible synonym of P. carditoides]; Deshayes, 1853: 208 [as a possible synonym of P. carditoides]; G. B. Sowerby II, 1854a:769–770, pl. 165, figs. 36–38 [as Venerupis]; Carpenter, 1857a:214 [as a possible synonym of P. carditoides]; Carpenter, 1857b:196, 203, 219, 224, 229, 284, 299 [as a possible synonym of P. carditoides]; Carpenter, 1864b:526, 528, 534, 592, 634, 641 [1872:12, 14, 20, 78, 120, 127] [as a synonym of P. carditoides]; Tryon, 1872:255, 257 [as a synonym of P. nivea]; Lamy, 1923a:282 [as a synonym of P. carditoides].
- Petricola gibba Middendorff, 1849. Middendorff, 1849:
 573–574 [1872:57–58], pl. 18, figs. 5–7; Deshayes, 1853:208; Carpenter, 1857b:196, 219, 223, 299 [as possible synonym of *P. carditoides*]; Carpenter, 1864b:534, 641 [1872:20, 127] [as a synonym of *P. carditoides*];

Explanation of Figures 8 to 12

Figures 8–12 Petricola (Petricola) caritoides (Conrad, 1837). Figure 8. P. gibba Middendorff, 1849; holotype; ZISP; length, 37 mm [rough scanned image, courtesy ZISP]. Figure 9. P. mirabilis Deshayes, 1853; holotype; BM(NH) 1966555; length, 35.9 mm. Figure 10. Saxicava abrupta Conrad, 1855; lectotype; USNM 1869; length, 20.5 mm. Figure 11. Petricola pedroana Conrad, 1855; original figure; length, 31 mm. Figure 12. CAS 102584; Carmel, Monterey Co., California; length, 4.8 mm; SEM image.

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				Pallial line-	Pallial line-				
	Ligament	Lunule/ escutcheon	Pallial sinus- depth/Rounding	bowed dorsally	confluence with sinus	Radial sculpture	Commarginal sculpture	Hinge teeth- RV/LV	Maximum length, mm
P. botula	deeply sunken	neither	moderate, rounded	оц	short distance	~ 90–100 fine, bifurcating	growth checks only	2/3	15.5
P. carditoides	deeply sunken	neither	moderate, rounded	оп	short distance	~ 130 fine, bifurcating	growth checks only	2/3; LV ant. card. lost in many adults	63.3
P. linguafelis	deeply sunken	neither	deep, rounded	yes	substantially	network of beads	growth checks only	2/3; RV with elongate posterior lat- eral ridge	7.3
P. lucasana	deeply sunken	neither	moderate, rounded	2	short distance	~ 40–60 fine, bifurcating	growth checks only	2/3; LV ant. card. lost in many adults; RV with low posteri- or lateral ridge	43.5
P. californiensis	shallow	neither	deep, rounded	slightly	substantially confluent or parallel	\sim 60; 12 anterior broadest	fine ribs	2/3; LV ant. card. not ev- ident in many adults	42.2
P. concinna	shallow	slight escutch- eon	moderate, rounded	оц	ou	~ 12; on anterior end; very fine posterodorsal ribs	lamellae	2/3	21.1
P. dactylus	shallow	neither	moderate, pointed	ou	оц	\sim 27; 12 anterior broadest	narrow, lamel- lar anteriorly	2/3	57.5
P. denticulata	slightly sunken posteriorly	neither	shallow-moder- ate, rounded to pointed	ou	о	~ 50; 13 anterior broadest	strong, dense	2/3; LV ant. card. lost in adults	42
P. rugosa	shallow	neither	moderate, rounded	slightly	о	\sim 40, strongest on both ends	growth checks only	2/2; no LV ant. card. evident at all	50
P. exarata	shallow	long, narrow es- cutcheon	moderate, rounded	yes	short distance	\sim 100 fine threads	growth checks only	2/3; LV ant. card. lost in adults; RV with posteri- or lateral ridge	15

Differentiating characters in Eastern Pacific petricolids

Table 2

	Maximum length, mm	2	30	18.5	42.5	80	60 in eastern Pac.; 71.3 in western Atl.
	Hinge teeth- RV/LV	2/3; teeth very delicate, fre- quently bro- ken	2/3	2/3	2/3; LV ant. car. lost in most adults; hinge often gerontic in adults	2/3	2/3
	Commarginal sculpture	irregular striae	growth checks only	lamellae	fine threads	growth checks only	fine threads
Continued.	Radial sculpture	low, obscure near ends in most	~ 50-60 fine, narrow	~ 50, finer posteriorly	~ 50 heavy, heaviest posteriorly	~ 8 scaly ribs anteriorly, \sim 20 posterior threads	~ 8 scaly ribs anteriorly, ~ 36 posterior threads
	Pallial line– confluence with sinus	short distance	substantially	short distance	ou	Ê	ог
	Pallial line- bowed dorsally	yes	yes	slightly	оц	ои	о
	Pallial sinus- depth/Rounding	moderate, rounded	moderate, rounded	moderate, rou <mark>n</mark> ded	moderate, rounded	deep, pointed	deep, pointed
	Lunule/ escutcheon	neither	neither	slight escutch- con	ncither	lunule	neither
	Ligament	shallow	shallow	shallow	deeply sunken	shallow	shallow
		P. hertzana	P. olssoni	P. scotti	C. robustum	P. cognata	P. pholadiformis

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Table 2

Tryon, 1872:256, 257 [as a synonym of *P. nivea*]; Arnold, 1903:154 [as a synonym of *P. carditoides*]; Lamy, 1923b:355 [as a variety of *P. carditoides*].

- Petricola mirabilis Deshayes, 1853. Deshayes, 1853:207; G.
 B. Sowerby II, 1854a:766, pl. 165, fig. 24 [as Venerupis]; Carpenter, 1857b:281; Tryon, 1872:257; G. B.
 Sowerby II, 1874b:pl. 1, fig. 4a, b [as Venerupis]; Lamy, 1923a:284; Lamy, 1923b:341–342.
- [non P. mirabilis Deshayes, auctt.]. Lischke, 1871:122; Habe, 1951:98; Habe, 1952:187; Habe, 1977:275.
- Saxicava abrupta Conrad, 1855. Conrad, 1855a:13; Conrad, 1857:824, pl. 3, figs. 25, 25a; Carpenter, 1864b:590 [1872:76] [as a probably synonym of *P. carditoides*]; Dall, 1898:835: [the following three references as a synonym of *P. carditoides*]; Dall, 1909a:124; Grant & Gale, 1931:355; Hertlein & Grant, 1972:283.
- Petricola pedroana Conrad, 1855. Conrad, 1855a:13–14; Conrad, 1857:824, pl. 3, fig. 24 [not "fig. 26," as implied by plate explanation; this figure is not even present on plate]; Carpenter, 1864b:590 [1872:76] [as similar to *P. ventricosa*]; [the next three references as a synonym of *P. carditoides*]; Grant & Gale, 1931:355; Woodring, 1938: 51; Hertlein & Grant, 1972:283.

Type material and localities: S. carditoides-Lost. The holotype, a right valve that measured 38 mm in length (Figure 3). Santa Barbara, Santa Barbara County, California (34.4°N); T. Nuttall, spring 1836. S. californica-Lost. The original figure measures 27 mm in length (Figure 4). Conrad had specimens from Santa Barbara, Santa Barbara County, California (34.4°N), and San Diego, San Diego County, California (32.7°N); both T. Nuttall, spring 1836. S. legumen-Lost. (P. Bouchet, e-mail, 3 January & 30 January 1996). The original figure measures 37 mm in length (Figure 5). California, from marine "marl." P. arcuata-MNHN, holotype, paired valves; length, 38.2 mm; height, 19.8 mm; thickness, 18.6 mm (Figure 6). California, from marine "marl." P. cylindracea-Lost. The holotype, paired valves, measured 20 mm in length, 22 mm in height, and 20 mm in thickness (Figure 7). California, from marine "marl." P. gibba-ZISP, holotype, paired valves; length, 37 mm (original measurement) (Figure 8). Sitka Island, Alaska (about 57°N); the original text cites Eschscholtz as collector, but the label specifies Wosnessenski. P. mirabilis-BM(NH) 1966555, holotype, paired valves; length, 35.9 mm; height, 23.7 mm; thickness, 23.7 mm (Figure 9). California; the label adds "Monterey, in sandstone, deep water" (36.6°N). S. abrupta-USNM 1869, lectotype here designated, a sealed pair separate from matrix, probably the specimen figured in Conrad (1857:pl. 3, fig. 25a); length, 20.5 mm; height, 12.9 mm; thickness, 10.5 mm (Figure 10). Paralectotypes, a smaller pair inside lectotype, and three whole pairs, one broken pair, and two valves imbedded in holes in rock matrix. This matrix may also be that in which the next species was found. San Pedro, Los Angeles County, California (33.7°N); Pleistocene; in cavities in rock. P. pedroana-Lost. Holotype, right valve (Figure 11). No size was specified; the figure in Conrad (1857) measures 31 mm in length. San Pedro, Los Angeles County, California (33.7°N); Pleistocene; in cavities in rock.

Description: Shell typically ovate, but variously shaped depending on nestling site, becoming elongate in some situations; anterior end short, rounded; posterior end subtruncate to rounded. Shell inflated, thick; beaks prominent. Without lunule or escutcheon. Surface completely covered with very fine (at least 130), somewhat divaricate radial ribs in uneroded specimens. Pallial sinus of moderate depth, broad, rounded, confluent with pallial line for a very short distance; pallial line not bowed dorsally (Figure 56). External and internal color white to tan; juveniles mottled with brown. Hinge heavy; right valve with a heavy anterior cardinal and a bifid posterior cardinal; left valve with a small anterior cardinal (lost in many adult specimens), a bifid central cardinal, and a narrow posterior cardinal. Ligament elongate, deeply sunken. Length to 63.3 mm [MNHN; Monterey, California]. A small pair showing fine sculpture is depicted with an SEM image in Figure 12.

Distribution and habitat: Sitka Island, Alaska (approximately 57°N) (type locality of *P. gibba*); Edna Bay, Kosciusko Island [CAS 105780] (55.9°N], and near Ratz Harbor, Prince of Wales Island [SBMNH 14224] (53.9°N), Alaska, to Punta Pequeña, Baja California Sur (26.2°N) [LACM 71-5, 71-6, 71-181], from the intertidal zone to 46 m, nestling in rocky areas. Orcutt (1919:40) and Dall (1921:44) reported this species from Bahía Magdalena, Baja California Sur, but I have been unable to find any material in collections from there. A single specimen in the CAS labeled has having come from Mazatlán, Sinaloa, Mexico [CAS 102501], requires additional verification, and a speciment labeled as having come from Kamchatka [MNHN] seems implausible. I have examined 516 lots.

There are many records of this species in the Pleistocene of central California (Woodring & Bramlette, 1951: 54; Valentine, 1958:690; Addicott, 1966:4), southern California (Santa Barbara-Valentine, 1961:389; Kennedy et al., 1993:347; northern Los Angeles-Woodring, in Hoots, 1931:120; Addicott, 1964:146; Playa del Rey-Willett, 1937:390; San Pedro-T. S. Oldroyd, 1914:82, 1925:6; Crickmay, 1929:631; DeLong, 1941:242, table at p. 244, Valentine, 1961:370, 372; Capistrano-Willett (1938:106); San Clemente-Valentine (1961:364); San Diego-Webb, 1937:345; Emerson & Addicott, 1953: 440; Valentine, 1960:163, 1961:360, 361; Valentine & Meade, 1961:10); San Nicolas Island-Vedder & Norris, 1963:46, 47), northern Baja California (Emerson, 1956: 339; Valentine, 1957:296, 1961:357; Emerson & Addicott, 1958:8; Addicott & Emerson, 1959:17; Emerson & Hertlein, 1960:3; Valentine & Meade, 1961:16; Valentine & Rowland, 1969:517), and central Baja California (Emerson, 1980:72).

There are also records in the late Pliocene of central California (Nomland, 1917:220; ?Woodring & Bramlette, 1951:90), Ventura (Waterfall, 1929: checklist col. 2; Woodring, in Winterer & Durham, 1962:304–305), the Los Angeles area (Moody, 1916:45; Soper & Grant, 1932:1060), Newport Bay (Zinsmeister, 1971:124), and San Diego (Hertlein & Grant, 1972:283–284).

Records of this species from the Miocene, such as Gale, in Preston (1931:15) and Woodring & Bramlette (1951:66, 90), are uncertain and may refer to *P. buwaldi* (see under *Choristodon robustum*).

Discussion: Conrad (1837) described this species twice in the same paper. Carpenter (1857a:214) acted as First Reviser in the sense of ICZN Code Art. 24 and made P. carditoides a synonym of P. californica. However, he later reversed his action and began using P. carditoides for the species, a course followed by all subsequent workers. Under the present Code, a petition to set aside his first action would be required. However, because use of P. carditoides has been universal for a century and because, in all likelihood, the next version of the Code will leave such questions entirely up to taxonomists working on particular groups (P. Tubbs, letter, 20 December 1995), a petition seems pointless. (This species is not to be confused with the Australian Venerupis carditoides Lamarck, 1818: 508, most recently placed in the venerid genus Timoclea [Lamprell & Whitehead, 1992:pl. 62].)

Petricola arcuata and P. cylindracea Deshayes, 1839, have long been regarded as synonyms. The type specimen of only one of these taxa survives. Saxicava legumen Deshayes, 1839, was suggested as a possible synonym by Dall (1898:835), but more recently it has been allocated to synonymy under *Hiatella* (Bernard, 1983:59). However, because Deshayes mentioned and illustrated a deep pallial sinus, it is far more likely to belong in synonymy here.

Petricola gibba is undoubtedly a synonym, and its holotype has been located. It remains the northern record by about 2° in latitide. Additional collecting in southeast Alaska may bring additional material from as far north as Sitka Island to light.

Petricola mirabilis, although described from California, was attributed to Japan by Lischke (1871), and subsequent workers did not question this. However, its holotype is a specimen of *P. carditoides*. In the meanwhile, the Japanese "*P. mirabilis,*" an evidently uncommon species with more prominent, zig-zag sculpture, was made the type species of the genus *Pseudoirus* Habe, 1951 (see discussion under the genus above).

Conrad's (1855a) *Petricola abrupta* was based on not infrequent specimens of this species with fairly eroded sculpture. However, the lectotype shows some of the characteristic fine radial ribs. Conrad's *S. pedroana* is certainly a synonym; its original description mentions fine Page 307

radial sculpture. Both species were found in cavities in the same rock.

Petricola buwaldi Clark, 1915, described from the Miocene of central California, was synonymized with *P. carditoides* by Bernard (1983), but it is instead a synonym of *Choristodon robustum* (see under same).

Young (1958) found the siphons of *Petricola carditoides* to be fused for half their length and capable of expansion to a distance equal to the shell length. The inhalent siphon has four rows of dendritic tentacles surrounded by a row of simple tentacles. The exhalent siphon has two rows of two rows of pinnate tentacles and one of simple tentacles. The inner demibranch is somewhat larger and extends farther forward than the outer. The animal is capable of modest expansion of its burrow by lateral pressure of the valves. D. P. Abbott & Hilgard (1987:194) figured living *Petricola carditoides*. A long, extensible foot was illustrated, as well as a terminal valvular membrane on the exhalent siphon and large labial palps.

Petricola (Petricola) linguafelis (Carpenter, 1857)

(Figures 13-16, 57)

- Rupellaria linguafelis Carpenter, 1857. Carpenter, 1857b: 244, 299, nomen nudum; Carpenter, 1857c:20; Carpenter, 1864b:620 [1872:106]; Lamy, 1923a:285; Keen, 1958:152; Brann, 1966:27, pl. 2, fig. 27; Keen, 1968: 394, 395, fig. 17, 399 [Petricola (Petricola)]; Keen, 1971:197 [as a synonym of P. exarata]; Bernard, 1983: 57 [as a synonym of P. exarata].
- "?Naranio" scobina Carpenter, 1857. Carpenter, 1857b:244, nomen nudum; Carpenter, 1857c:529; Tryon, 1872:258; Lamy, 1923b:341; Brann, 1966:29, pl. 4, fig. 680; Keen, 1968:394, 395, fig. 18, 399, pl. 55, fig. 11 [as a synonym of P. (P.) linguafelis; First Revision]; Keen, 1971: 197 [as a synonym of P. (P.) exarata]; Bernard, 1983: 57 [as a synonym of P. (P.) exarata].
- *Cypricardia noemi* de Folin, 1867. de Folin, 1867:62–63 [repr.:24–25], pl. 4, figs. 1, 2; de Folin & Périer, 1867: 8; Kisch, 1960:162; Keen, 1971:197 [as a synonym of *P. (P.) exarata*]; Bernard, 1983:57 [as a synonym of *P. (P.) exarata*].

Type material and localities: *R. linguafelis*—BM(NH) Carpenter Mazatlán Collection tablet 72, species 27, **lectotype here designated**, the largest paired valves; length, 4.0 mm; height, 2.7 mm; thickness, approx. 2.0 mm (Figure 13). BM(NH), paralectotypes, three additional pairs. A fifth pair cited by Carpenter & Keen (1968) is no longer present. USNM 715644, paralectotypes, two pairs and two fragments. Mazatlán, Sinaloa, Mexico (23.2°N); nestling in valves of Chamidae and *Spondylus calcifer* Carpenter, 1857; F. Reigen. *N. scobina*—BM(NH) Carpenter Mazatlán Collection tablet 2516, species 680, holotype, a right valve; length 4.4 mm; height, 3.5 mm; thickness approx. 1.0 mm (Figure 14). A left valve added to slide later is a Carpenter voucher specimen. USNM 716248, one left valve and one broken pair, additional Carpenter



voucher specimens. Mazatlán, Sinaloa, Mexico (23.2°N); nestling in a valve of *Spondylus calcifer* Carpenter, 1857; F. Reigen. *C. noemi*—BM(NH) 196459, **lectotype here designated**, paired valves still sealed closed; length, 2.5 mm; height, 1.9 mm; thickness, 1.4 mm (Figure 15). De Folin's figures show that he had at least one additional specimen. Archipelago de las Perlas, Panamá (approximately 8.4°N).

Description: Shell ovate; anterior end very short, rounded; posterior end rounded. Shell inflated, thin; beaks prominent. Without lunule or escutcheon. Sculpture of a network of very small beads. Pallial sinus deep, broad, dorsally directed, rounded, overlapping pallial line for a substantial distance; pallial line bowed dorsally, sometimes in discontinuous patches (Figure 57). Hinge teeth robust for size; right valve with a narrow anterior cardinal and a bifid posterior cardinal, and with an elongate posterior lateral ridge below hinge margin; left valve with a tiny anterior cardinal, a bifid central cardinal, and a small posterior cardinal. Ligament of medium length, deeply sunken; nymph stout. Color white externally and internally. Length to 7.3 mm [MNHN; La Puntilla, Guavas Province, Ecuador]. A SEM image is provided of the external scupture (Figure 16).

Distribution and habitat: Bahía Pulmo, Baja California Sur (23.4°N) [LACM 66-19.56], and Mendia, Sinaloa (23.7°N) [USNM 532732], Mexico, to Salinas, Guayas Province, Ecuador (2.2°S) [LACM 70-9; CAS 102586], from the intertidal zone to 3 m, in rocky areas. I have examined 23 lots.

Discussion: This species is thus far known from several, widely distributed lots. It has a very distinctive beaded sculpture that sets it apart from the young of other taxa, such as *P. lucasana*, which have radial rays. However, the affinities of this small-sized species seem to be with *Petricola (Petricola)*, of which it may be a pedogenetic derative.

I have examined a single left valve from the western Atlantic that is similar to this species. It was collected on Abaco Island in the Bahamas (Redfern Collection), and it may either be a form of *P*. (*P*.) lapicida (Gmelin, 1791) or a new species. It differs from *P. linguafelis* in having a thinner, more delicate hinge, and the anterior and central cardinals are fused dorsally; they are separate in *P. linguafelis*.

Petricola (Petricola) lucasana Hertlein & Strong, 1948

(Figures 17-20, 58)

Petricola (Petricola) lucasana Hertlein & Strong, 1948.
Hertlein & Strong, 1948:194, 197, 198, pl. 2, figs. 4, 9;
Keen, 1958:150, 151, fig. 345; Keen, 1971:197, 198, fig. 477; Bernard, 1983:57 [Petricola (Petricola)].

Petricola (Naranio) charapota Olsson, 1961. Olsson, 1961: 317, pl. 54, fig. 7; Keen, 1971:196, 197 [Petricola (Petricola)]; Bernard, 1983:57 [Petricola (Petricola)].

Type materials and localities: *P. lucasana*—CAS 06,5562, holotype, paired valves; length, 24.6 mm; height, 24.9 mm; thickness 16.6 mm (Figure 17). Cabo San Lucas, Baja California Sur (22.9°N). *P. charapota*—ANSP 218907, holotype, left valve; length, 30.1 mm; height, 21.0 mm; thickness, 9.4 mm (Figure 18). "Charapota" [Charapotó], Manabi Province, Ecuador (0.8°S).

Description: Shell ovate, sometimes as high or higher than long; anterior end short, rounded; posterior end subtruncate. Shell inflated, fairly thick; beaks prominent. Without lunule or escutcheon. Sculpture of many (more than 60) divaricating ribs in small specimens, becoming more divaricating and sometimes becoming fewer in number (about 40) in large specimens; overlain by secondary lamellose radial ribs on posterior slope in some specimens. Pallial sinus of moderate depth, broad, not dorsally directed, rounded, overlapping pallial line for a very short distance; pallial line not bowed dorsally (Figure 58). Hinge robust; right valve with a small anterior cardinal and a slightly bifid posterior cardinal, and with a low posterior lateral ridge; left valve with a small anterior cardinal, which may be lost in adult, a narrow, slightly bifid central cardinal, and a thin posterior cardinal. Ligament medium in length, deeply sunken; nymph heavy. White to tan externally; reddish-brown internally, especially on hinge and around margins of valves. Length to 43.5 mm [Skoglund Collection; Cabo Tepoca, Sonora, Mexico]. A small specimen is depicted by an SEM image (Figure 19).

Explanation of Figures 13 to 20

Figures 13–16. Petricola (Petricola) linguafelis (Carpenter, 1857). Figure 13. Rupellaria linguafelis; lectotype; BM(NH) Carpenter Collection 72(27); length, 4.0 mm. Figure 14. Naranio scobina Carpenter, 1857; holotype; BM(NH) Carpenter Collection 2516(680); length, 4.4 mm. Figure 15. Cypricardia noemi de Folin, 1867; lectotype; BM(NH) 196459; length, 2.5 mm. Figure 16. LACM 75-55; San Carlos, Golfo de Panama; length, 3.9 mm; SEM image. Figures 17–20. Petricola (Petricola) lucasana Hertlein & Strong, 1948. Figure 17. P. lucasana; holotype; CAS 065562; length, 24.6 mm. Figure 18. P. charapota Olsson, 1961; holotype; ANSP 218907; length, 30.1 mm. Figure 19. CAS 102518; Puerto Peñasco, Sonora, Mexico; length, 22.8 mm. Figure 20. CAS 102518; length, 4.6 mm; SEM image.

[←]



Distribution and habitat: Throughout the Golfo de California from its head at Puerto Peñasco, Sonora, Mexico (31.3°N) [SBMNH 27231 and other lots; CAS 102518 and other lots], to Cabo San Lucas, Baja California Sur (type locality of *P. lucasana:* USNM 75035), south to Punta Quepos, Puntarenas Province, Costa Rica (9.4°N) [LACM 72-58.57], and at Charapotó, Manabi Province, Ecuador (0.8°S) [type locality of *P. charapota*], and Salinas, Guayas Province, Ecuador (2.2°S) [CAS 105779], from the intertidal zone to 30 m, in calcareous substrata, such as corals. Also present on Pleistocene terraces in Ecuador [MNHN]. I have examined 73 lots.

Discussion: Juvenile specimens of this species are white or tan and do not develop their characteristic deep red color until about 6–7 mm. Their heavy hinge and deeply sunken ligament are readily apparent even in very small specimens.

This species is somewhat similar to the Caribbean and IndoPacific *P. (P.) lapicida* (Gmelin, 1791), from which it differs in being heavier, having a more variable outline, being red within, and in less frequently having secondary posterior radial frills.

The unique type of *Petricola charapota* from Ecuador has its beaks very close to the anterior end. In the Golfo de California, *Petricola (P.) lucasana* tends to assume an oval outline, sometimes becoming higher than long. However, some of the sparse material available of *P. (P.) lucasana* from Costa Rica and elswhere also have beaks relatively close to the anterior end, and even some specimens of this species from the Golfo de California can also have this morphology. Indeed, *Petricola (P.) lucasana* has been reported from Ecuador (Hoffstetter, 1952: 34), but none of this material seems to be preserved in the major collections in the United States.

Petricola millestriata Brown & Pilsbry, 1913 (pp. 516– 517, pl. 26, fig. 2), from the Miocene of Panamá, may be ancestral to this species, but it is as yet known from a single, now-lost specimen (Woodring, 1982:709).

Subgenus Petricolirus Habe, 1951

Petricolirus Habe, 1951:95–96, pl. 15, figs. 4, 5; 1952:188.
Type species (original designation); Petricola aequistriata G. B. Sowerby II, 1874a:pl. 3, fig. 19. Recent, Japan.

Members of this subgenus have an elongate shape and

radial sculpture that is generally more conspicuous than that in *Petricola*, *s.s.* and is neither divaricate nor zig-zag, and the ligament is not sunken. Of the species that are tentatively included here, *Petricola californiensis*, *P. concinna*, *P. dactylus*, *P. denticulata* have each been included within *Petricolaria* because of their elongate shape, but a narrower concept of that genus is used here.

Petricola (Petricolirus) californiensis Pilsbry & Lowe, 1932

(Figures 21, 59)

- Petricola californiensis Pilsbry & Lowe, 1932. Pilsbry & Lowe, 1932:97–99, pl. 13, figs. 7–9, text-fig. 6; Burch, 1944:19–20 [Petricola (Rupellaria)]; Bernard, 1983:57 [Petricola (Petricolaria)].
- Petricola denticulata G. B. Sowerby I, 1834. auctt., non G.
 B. Sowerby I, 1834. Dall, 1900b:121–122 [in part]; Arnold, 1903:155–156 [Petricola (Petricolaria)]; Dall, 1921:44 [in part]; Willett, 1931:39, pl. 17, fig. 3.
- "Petricola tenuis A. Adams," non P. tenuis G. B. Sowerby I, 1834. Jordan, 1924:153

Type material and locality: *P. californiensis*—ANSP 114337, holotype, paired valves; length, 26.5 mm; height, 12.2 mm; thickness, 10.5 mm (Figure 21). Paratypes, two additional pairs, 25.9 mm and 24.3 mm in length. San Pedro, Los Angeles County, California (33.7°N).

Description: Shell ovate-elongate; anterior end short, rounded; posterior end elongate, rounded. Shell inflated, thin; beaks somewhat inflated. Without lunule or escutcheon. Sculpture of approximately 60 radial ribs, of which the 12 most anterior are broadest, the rest becoming finer toward posterior end, and with fine commarginal ribs. Hinge teeth relatively small; right valve with a narrow anterior cardinal tooth and a slightly bifid posterior cardinal; left valve with a small anterior cardinal that is not apparent in most large specimens, a bifid central cardinal, and an elongate posterior cardinal. Ligament elongate, on a narrow nymph. Pallial sinus deep, of moderate width, rounded, closely paralleling or confluent with pallial line for a substantial distance; pallial line somewhat bowed dorsally (Figure 59). White to tan externally and internally, sometimes with brownish-purple patches externally on posterior slope, especially in small specimens. Length to 42.2 mm [CAS 105776; Long Beach, Los Angeles County, California].

Explanation of Figures 21 to 24

Figure 21. *Petricola (Petricolirus) californiensis* Pilsbry & Lowe, 1932; holotype; ANSP 114337; length, 26.5 mm. Figure 22. *Petricola (Petricolirus) concinna* G. B. Sowerby I, 1834; lectotype; BM(NH) 1966554/1; length, 21.1 mm. Figures 23, 24. *Petricola (Petricolirus) dactylus* G. B. Sowerby I, 1823. Figure 23. *P. dactylys*; holotype; BM(NH) 1995215; length, 57.5 mm. Figure 24. *P. patagonica* d'Orbigny, 1845; lectotype; BM(NH) d'Orbigny Coll. 558, 1854.12.4.708/1; length, 42.9 mm.

(

Distribution and habitat: Bolinas, Marin County (37.9°N) [ANSP 39870], and Pacific Grove, Monterey County (36.6°N) [CAS 102867], California, both probably the result of larval settlement in particularly warmwater years; established populations from Coal Oil Point, Santa Barbara County, California (34.4°N) [CAS 39055], to Bahía Magdalena, Baja California Sur (24.6°N) [LACM 49-57], and in the west coast of Mexico from Puerto Peñasco (31.2°N) [LACM 152162] and Playa Cochore, Guaymas (27.9°N) [SBMNH 137767; CAS 105777], Sonora, to San Blas, Nayarit (21.5°N) [SBMNH 32588], and probably to Bahía Ventosa, Oaxaca, Mexico (16.2°N) [SBMNH 142892], from the intertidal zone to 64 m, nestling in a variety of substrata: driftwood, including in teredinid burrows, kelp holdfasts, and clumps of annelid worm tubes. Material in collections labeled as having some from Washington [LACM 56919, 56920; FMNH 142805] probably represents locality errors. I have examined 251 lots.

Also present in the Pleistocene of southern California (Playa del Rey—Willett, 1937:390; San Pedro—DeLong, 1941:242, table at p. 244; Valentine, 1961:370; Newport Bay—Bruff, 1946:232; Kanakoff & Emerson, 1959:24), and northern Baja California (Valentine, 1957:296). The only record of this species in the Pliocene of southern California (Soper & Grant, 1932:1057, taken from Cooper, in Watts, 1897:79) is more likely to have been based on a *Calyptogena* (Woodring, 1938:51).

Discussion: Early records of this species in southern California were as the Panamic species *Petricola denticulata* (for comparisons, see under that species). This species is most similar to *Petricola olssoni* (for comparisons, see under that species).

Arnold (1903:155) synonymized *P. pedroana* Conrad, 1855, with *P. californiensis* [as "*P. denticulata*"]. However, Conrad's species, of which the holotype is lost, was more likely to have been a specimen of *P. carditoides* (see under that species).

Based on specimens so labeled in the California Academy of Sciences, its seems likely that the material cited by Jordan (1924) as "*Petricola tenuis* A. Adams" from Laguna San Ignacio, Baja California Sur, were specimens of *P. californiensis* (see also Discussion under *P. rugosa*, for possibly related confusion about the species-name *tenuis*).

It has not previously been recognized that *P. californiensis* also occurs on the northwest coast of Mexico, from Sonora to Nayarit, material in collections having been identified as *P. denticulata* or *P. exarata*.

Young specimens of *Petricola californiensis* may be distinguished from *P. hertzi* in being more elongate and more produced both anterior and posteriorly, and in attaining a larger size. *Petricola californiensis* is also more heavily sculptured and has a heavier hinge.

Petricola pectorosa (Conrad, 1834:130) [see also Con-

rad, 1838:18, pl. 10, fig. 3; synonym: *P. (Claudiconcha)* grinnelli Olsson, 1914:54–55, pl. 11, figs. 7–10] from the Pliocene and Pleistocene of eastern North America may be ancestral to this species. It is smaller and has more prominent radial sculpture.

Petricola (Petricolirus) concinna G. B. Sowerby I, 1834

(Figures 22, 60)

Petricola concinna G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:46; d'Orbigny, 1846:549; Deshayes, 1853:214; G. B. Sowerby II, 1854b:773, pl. 166, fig. 3; Tryon, 1872:256; G. B. Sowerby II, 1874a:pl. 1, fig. 3; Dall, 1909b:269; Lamy, 1923b:347; Olsson, 1961:527, pl. 54, fig. 4 [Petricola (Petricolaria)]; Keen, 1971:198, 199, fig. 479 [Petricola (Petricolaria)]; Bernard, 1983:57 [Petricola (Petricolaria)].

Type material and locality: *P. concinna*—BM(NH) 1966554/1, **lectotype here designated**, left valve; length, 21.1 mm; height, 10.2 mm; thickness, 5.0 mm (Figure 22). BM(NH) 1966544/2, paralectotype, pair, 19.6 mm in length. The lectotype selected seems to have been the specimen figured by G. B. Sowerby II (1854b). Montecristi [Manta], Manabi Province, Ecuador (1.0°S), in hard clay at low water; H. Cuming.

Description: Shell elongate; anterior end short, rounded; posterior end produced, tapered, truncate to bluntly pointed, prolonged beyond inner shell margin by outer shell layer, foliate within; posterodorsal margin slightly flared posterior to ligament, with right valve slightly overlapping left. Shell inflated, average in thickness; beaks small. Lunule absent; very small escutcheon posterior to ligament. Sculpture of heavy, well-spaced commarginal ribs, which are very lamellar and sometimes upturned on posterior end and made scabrous by about 12 radial ribs on anterior end. Pallial sinus of moderate depth and width, rounded, slightly bowed dorsally, completely detached from pallial line (Figure 60). Hinge teeth small; right valve with bifid anterior and posterior cardinals; left valve with a tiny anterior cardinal, a bifid central cardinal, and a short posterior cardinal. Ligament short, shallow; nymph thin. White externally and internally. Length to 21.1 mm (lectotype).

Distribution and habitat: Esmeraldas, Esmeraldas Province (1.0°N) (Olsson, 1961: pl. 54, fig. 4; PRI 25774); Manta, Manabi Province (1.0°S) [type locality], to La Libertad (2.2°S) [LACM 33-15.13], Guayas Province, and Bahía Bartolomé, Isla Bartolomé, Islas Galápagos (0.3°S) [LACM 71-50.1], Ecuador, from the intertidal zone to 18 m. Records from farther south, such as Perú (d'Orbigny, 1846:549) and Arica, Tarapacá Province, Chile (Deshayes, 1853:214), are doubtful and require further confirmation. I have examined eight lots.

Discussion: This is a distinctive but rare species. For

comparisons with *P. scotti*, see under that species. Small specimens of some other taxa may develop a few, low commarginal frills on the posterior slope, including *P. olssoni*, which can be differentiated by its oval outline and broad, deep pallial sinus.

Petricola (Petricolirus) dactylus G. B. Sowerby I, 1823

(Figures 23, 24, 61)

- Petricola dactylus G. B. Sowerby I, 1823. G. B. Sowerby I, 1823:Petricola sp. 3; Deshayes, 1853:213; Tryon, 1872: 256; ?G. B. Sowerby II, 1874a:pl. 3, fig. 4; Lamy, 1923b:345–346 [in part] [Petricola (Petricolaria)].
- [non Petricola dactylus auctt; see under P. denticulata and Petricolaria pholadiformis].
- Petricola patagonica d'Orbigny, 1845. d'Orbigny, 1845: 547–548, pl. 82, figs. 7–10; Lamy, 1923b:346–347 [Petricola (Petricolaria)]; Carcelles, 1944:288, pl. 13, fig. 101 [Petricola (Petricolaria)]; Carcelles, 1950:80, pl. 4, fig. 77 [Petricolaria]; Carcelles & Williamson, 1951: 343 [Petricolaria]; Figueiras & Sicardi, 1969:364–365, 376, pl. 4, fig. 52 [Petricola (Petricolaria)].
- ?Petricola chiloensis Philippi, 1845. Philippi, 1845:53; [the next four references as a synonym of *P. rugosa*]; Dall, 1909b:289; Lamy, 1923b:351; Soot-Ryen, 1959:60; Bernard, 1983:57.

Type material and localities: P. dactylus-BM(NH) 1995215, holotype, paired valves; length, 57.5 mm; height, 29.7 mm; thickness, 26.9 mm (Figure 23). Original locality unknown; here restricted to southern Argentina. P. patagonica-BM(NH) d'Orbigny collection 558, 1854.12.4.708/1, lectotype here designated; length, 42.9 mm; height 21.0 mm; thickness, 18.1 mm (Figure 24). BM(NH) 1954.12.4.708/2-4, paralectotypes, three other pairs, 37.1 mm, 34.6 mm, and 33.9 mm in length. Ensenada de Ros, south of the mouth of Río Negro, Río Negro Province, Argentina (approximately 41.0°S), in calcareous rocks. P. chiloensis-Probably lost. Not in MNH-U (R. Kilias, in correspondence, 20 January 1996). The original material measured 8.8 mm in length, 6.6 mm in height, and 4.4 mm in thickness. Isla Chiloé, Chiloé Province, Chile (approximately 43°S); in roots of fucoid algae and in barnacle valves.

Description: Shell ovate-elongate; anterior end short, slightly produced, somewhat pointed; posterior end sharp-ly rounded. Shell inflated, moderately to very thick-shelled; beaks somewhat inflated. Without lunule or escutcheon. Sculpture of approximately 12 strong, broad radial ribs on anterior end and about 15 on central slope, become obsolete and narrower on posterior slope; with narrow commarginal ribs that form lamellae on radial ribs of anterior end; commarginal ribs dominant in some material. Pallial sinus narrow, of moderate depth, pointed anteriorly, completely detached from pallial line; pallial line not bowed dorsally (Figure 61). Hinge teeth robust; right valve with a small anterior cardinal and a narrow,

bifid posterior cardinal; left valve with a small anterior cardinal, a bifid central cardinal, and a small posterior cardinal. Ligament short, not sunken; nymph robust. White to tan externally, with a slight flush of magenta on internal surface. Length to 57.5 mm (type specimen).

Distribution and habitat: Maldonado, Maldonado Province, Uruguay (34.9°S) [ANSP 368239], and Punta Tubul, Arauco Province, Chile (37.3°S) [UCMP D3713, D5719], to Punta Arenas, Magallanes Province, Chile (53.2°S) [SBMNH 132931, 133419; LACM 62-24.1], from the intertidal zone to 20 m. A single record from Bahía Orange, Isla Hoste, Magallanes Province, Chile (55.5°S) [USNM 17647], is improbable and requires verification. I have examined 32 lots.

It is present in the Pleistocene of southern Argentina (Feruglio, 1933: 40, 62, 65, 67, 70, 72, 76, 160, 170).

Discussion: The name *P. dactylus* was misapplied to specimens of *Petricolaria pholadiformis* (Lamarck, 1818) from the northwestern Atlantic (see under that species). As a consequence, its proper place as a senior synonym of *P. patagonica*, confirmed here by the discovery of its probable holotype, has been overlooked.

Based on the locality, it is possible that *Petricola chiloensis* belongs in synonymy here. This species was never illustrated, and the type material is presumably lost. Philippi described *P. chiloensis* as being small, ovate, inflated, with radial striae and "without prominent features." On the other hand, it is possible that subsequent records of Philippi's taxon, such as those of Hupé (1854), are based on specimens of *P. rugosa*.

This species is most similar to *P. denticulata*, differing in lacking radial sculpture on the posterior slope, lacking brown color, attaining a larger size, and having a narrower pallial sinus.

d'Orbigny (1845:548, pl. 82, fig. 8) briefly discussed and figured the soft parts of *Petricola dactylus* G. B. Sowerby I, 1823 [as "*P. patagonica*"]. He described the animal as being yellowish, the viscera reddish, and the siphons as being partly fused and stained brown. He figured the ctenidia as being elongate, but he did not depict the labial palps.

Petricola (Petricolirus) denticulata G. B. Sowerby I, 1834

(Figures 25-28, 62)

Petricola denticulata G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:46–47; d'Orbigny, 1846:549; Troschel, 1852: 205; Deshayes, 1853:213–214; G. B. Sowerby II, 1854b:773, pl. 166, figs. 6, 7; Fischer, 1857:322, 326–327; Carpenter, 1857b:244, 297, 299; Tryon, 1872:256 [Petricola (Petricolaria)]; G. B. Sowerby II, 1874a:pl. 2, fig. 9; Dall, 1909b:269; Lamy, 1923b:347–349 [Petricola (Petricolaria)]; Grant & Gale, 1931:356–357 [in part]; Pilsbry & Lowe, 1932:98–99, pl. 13, figs. 1–3; I.



Explanation of Figures 25 to 28

Figures 25–28. *Petricola (Petricolirus) denticulata* G. B. Sowerby I, 1834. Figure 25. *P. denticulata*; lectotype; BM(NH) 199518/1; length 33.1 mm. Figure 26. *P. denticulata abbreviata* G. B. Sowerby I, 1834; lectotype; BM(NH) 1995219/1; length, 28.4 mm. Figure 27. *P. peruviana* Jay, 1839; lectotype; AMNH 56118; length, 27.2 mm. Figure 28. *P. ventricosa* Deshayes, 1853; lectotype; length, 30.9 mm.

S. Oldroyd, 1925:163 [in part]; Keen, 1958:152, 153, fig. 347 [*Petricola (Petricolaria)*]; Olsson, 1961:313–314, pl. 54, fig. 1 [*Petricola (Petricola)*]; Keen, 1971: 199, 200, fig. 481 [*Petricola (Rupellaria)*]; Bernard, 1983:57 [*Petricola (Rupellaria)*].

- Petricola denticulata abbreviata G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; Carpenter, 1857c:19.
- *Venerupis peruviana* Jay, 1839. Jay, 1839:13, 113, pl. 1, figs. 14, 15; Deshayes, 1853:212 [as a synonym of *P. pholadiformis*]; Lamy, 1923a:282; Lamy, 1923b:350 [as a probable synonym of *P. denticulata*]; Keen, 1958:152 [as a synonym of *P. denticulata*]; Keen, 1971:199 [as a

synonym of *P. denticulata*]; Bernard, 1983:57 [as a synonym of *P. denticulata*].

Petricola ventricosa Deshayes, 1853 [non Krause, 1848]. Deshayes, 1853:214 [cited here as "Proc. Zool. Soc.," but not occurring in that serial]; Carpenter, 1857b:244, 299 [as a possible synonym of *P. denticulata*]; Carpenter, 1857c:19; Carpenter, 1864b:668 [1872:154]; Tryon, 1872:256, 258 [as a synonym of *P. denticulata*]; G. B. Sowerby II, 1874a:pl. 3, fig. 23; [the following five references as a synonym of *P. denticulata*]; Dall, 1909b: 289; Lamy, 1923b:348; Keen, 1958:152; Keen, 1971: 199; Bernard, 1983:57.

- [non Petricola ventricosa Krause, 1848:2, a synonym of the South African tellinid Gastrana abildgaardiana (Spengler, 1798)].
- Petricola dactylus G. B. Sowerby I. auct., non G. B. Sowerby I, 1823. ?Carpenter, 1857b:232, 299, 352.

Type material and localities: P. denticulata—BM(NH) 1995218/1, lectotype here designated, paired valves; length, 33.1 mm; height, 15.7 mm; thickness, 14.6 mm (Figure 25). BM(NH) 1995218/2-3, paralectotypes, two other pairs, 33.6 m and 33.4 mm in length. The lectotype selected was the syntype closest to the originally stated measurement of 1.3 poll. [= 33.0 mm]. Paita, Piura Province, Perú (5,1°S); in hard clay and stones at low water; H. Cuming. P. denticulata abbreviata-BM(NH) 1995219/1, lectotype here designated, paired valves; length, 28.4 mm; height, 14.5 mm; thickness, 13.1 mm (Figure 26). BM(NH) 1995219/2-4, paralectotypes, three other pairs, 13.5 mm, 31.5 mm, and 32.6 mm in length. The lectotype selected was the syntype closest to the originally stated length of 1.1 poll. [= 27.9 mm]. Isla de La Plata, Manabi Province, Ecuador (1.3°S); in stones at low water, H. Cuming. P. peruviana-AMNH 56118, lectotype (Richards & Old, 1969:14, as "holotype"), paired valves; length, 27.2 mm; height, 11.8 mm; thickness, 11.8 mm (Figure 27). AMNH 226533, paralectotypes, two other pairs, 31.2 mm and 29.3 mm in length. The lectotype seems to be the originally figured specimen. The statement in Boyko & Sage (1996:28) that the Richards & Old lectotype designation was not valid is incorrect. Peru. P. ventricosa-BM(NH) 1966556/1, lectotype here designated, paired valves; length 30.9 mm; height, 19.9 mm; thickness, 16.1 mm (Figure 28). BM(NH) 1966556/2-3, paralectotypes, two valves, 33.3 mm and 32.1 mm in length. Golfo de California; H. Cuming.

Description: Shell elongate; anterior end short, somewhat produced; broadly to sharply rounded posteriorly. Shell inflated, moderately to very thick-shelled; beaks low. Without lunule or escutcheon. Sculpture of strong, dense, lamellar commarginal ribs and about 50 strong radial ribs, of which approximately the 13 anteriormost are prominent and broadest, the rest becoming almost obsolete medially and narrow posteriorly. Pallial sinus short to moderate in depth, of moderate width rounded to pointed anteriorly, completely detached from pallial line; pallial line not bowed dorsally (Figure 62). Hinge teeth robust; in right valve with a pointed anterior cardinal and a bifid posterior cardinal; in left valve with a tiny anterior cardinal that is generally lost in adult, a central cardinal bifid, and a lamellar posterior cardinal. Ligament elongate, on a well-developed nymph, slightly sunken below hinge margin posteriorly. White to tan externally; interior often with brown to purplish-brown patches on posterior end, sometimes on also anterior end and along dorsal and ventral margins. Length to 42.0 mm [CAS 102588; Boca de Barranca, Puntarenas Province, Costa Rica].

Geographic distribution and habitat: Bahía Santa Maria, Pacific coast of Baja California Sur (24.8°N) [USNM 264785, 269067], into and throughout the Golfo de California to its northern end at Puerto Peñasco, Sonora, Mexico (31.5°N) [LACM 41-1], south to Bayovar, Piura Province, Perú (5.8°S) [CAS 105775, UMML 30.9589], from the intertidal zone to 22 m, in soft rock. A record by Lamy (1930:96) at "Punta," presumably La Punta near Callao, Lima Province, Peru (approximately 12°S), is suspect and requires verification. A specimen from an old collection labled as having come from Isla Chiloé, Chiloé Province, Chile (MCZ 316109), probably represents a labeling error. I have examined 181 Recent lots. This species is also recorded in the Pleistocene of Ecuador (Hoffstetter, 1948:78).

Discussion: *Petricola denticulata abbreviata* was based on proportionately shorter specimens than the nominal subspecies. A still shorter specimen is figured by Olsson (1961:pl. 54, figs. 1a, b). This named variety has been overlooked in most subsequent synonymies.

Lamy (1923b) was the first to recognize that *Venerupis* peruviana Jay was probably a synonym of this species, and Tryon (1872) was the first to conclude that *P. ven*-tricosa Deshayes, based on inflated specimens, was a synonym.

Lamy (1923b) incorrectly placed *Psephis tellimyalis* Carpenter, 1864, in synonymy here; its type specimen is a *Halodakra* [Bernardinidae], and the *Petricola* for which this name has been used is here described as *P. hertzi*. Lamy (1923b) also regarded *P. costata* Philippi, 1849 [*non* Lamarck, 1801], as a variety of *P. denticulata*. However, because Philippi's description calls for material without radial ribs on the anterior slope, his taxon, described from an unknown locality, is more likely to have been a synonym of *P. rugosa* G. B. Sowerby I, 1834.

Most juvenile specimens of *P. denticulata* have more prominent radial sculpture, the commarginal sculpture becoming stronger with age.

Records of this species from southern California were based on material of *P. californiensis* Pilsbry & Lowe, 1932. The latter has a thinner, less colorful shell, a more rounded anterior end, less rugose, more predominantly radial sculpture, a more elongate pallial sinus, smaller teeth, and a less developed nymph.

Fischer (1857:322, 326–327) noted that *P. denticulata* has an elongate foot, small, elongate, fairly equal demibranchs, and very elongate labial palps.

Petricola (Petricolirus) rugosa G. B. Sowerby I, 1834

(Figures 29-31, 63)

Petricola rugosa G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; d'Orbigny, 1846:548; Deshayes, 1853:213; Hupé, 1854:345; Tryon, 1872:257, 258 [as a synonym of *P. nivea* "(Chemnitz, 1785)"]; Philippi, 1887:153,



pl. 25, fig. 11; Dall, 1909b:270; Lamy, 1923b:351–352 [*Petricola (Petricolaria)*]; Carcelles & Williamson, 1951:343; Soot-Ryen, 1957:8–9; Soot-Ryen, 1959:60; Marincovich. 1973:13 [in part], fig. 17 [fig. 18 = *P. olssoni*]; Bernard, 1983:57 [*Petricola (Petricolaria)*].

- Petricola tenuis G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; d'Orbigny, 1846:548; Troschel, 1852:204; Deshayes, 1853:215; Tryon, 1872:257, 258 [as a synonym of *P. nivea*]; Dall, 1909b:289 [as a synonym of *P. rugosa*, thus acting as First Reviser]; Lamy, 1923b:351 [as a synonym of *P. rugosa*]; Bernard, 1983:57 [as a synonym of *P. rugosa*].
- ?Petricola costata Philippi, 1849 [non Lamarck, 1801]. Philippi, 1849:163; Tryon, 1872:256 [as a synonym of P. nivea]; Lamy, 1923b:348–349 [as a variety of P. denticulata]; Bernard, 1983:57 [as a synonym of P. rugosa].
- [non Petricola costata Lamarck, 1801:121, = P. lapicida (Gmelin, 1791)]
- ?Petricola ovata Troschel, 1852. Troschel, 1852:204–205; Dall, 1909b:289 [as a synonym of *P. rugosa*]; Bernard, 1983:57 [as a possible synonym of *P. olssoni*].
- ?Petricola chiloensis Philippi, auctt, ?non Philippi, 1845. Hupé, 1854:345.

?[non Philippi, 1845:53]

- *Laxicava* [sic for *Saxicava*] *calderensis* Conrad, 1855. Conrad, 1855b:286; Philippi, 1887:286, pl. 25, fig. 13.
- Petricola rhyssodes Philippi, 1887. Philippi, 1887:154, pl. 25, fig. 12; Bernard, 1983:47 [as a synonym of P. rugosa].
- Petricola nivea (Gmelin, 1791), auctt., non Mytilus niveus Gmelin, 1791. G. B. Sowerby II, 1854b:773, pl. 166, figs. 13, 14; G. B. Sowerby II, 1874a:pl. 2, fig. 8; Lamy, 1908:51.

[non Mytilus nivea Gmelin, 1791:3358, ex Chemnitz ms]

Type material and localities: *P. rugosa*—Lost. None of the several lots of this species in BM(NH) can be confidently identified as the type material of this taxon. The original specimens measured: length, 35.6 mm; height, 17.8 mm; thickness, 14.0 mm. Concepción, Concepción Province, Chile (36.7°S), in barnacles at 3–7 fms. [5–13 m], H. Cuming. *P. tenuis*—BM(NH) 1995217/1, **lecto-type here designated**, paired valves; length, 26.0 mm; height, 12.9 mm; thickness, 11.2 mm (Figure 29). BM(NH) 1995217/2-3, paralectotypes, two other pairs, 23.1 mm and 19.0 mm in length. The lectotype selected is the pair closest to the originally stated length of 25.4 mm. Lambayeque, Lambayeque Province (6.7°S), and Pacasmayo, La Libertad Province (7.4°S), Perú; in hard clay at low water; H. Cuming. *P. costata* Philippi—Probably

lost. Not in MNH-U (R. Kilias, in correspondence, 20 January 1996). The original specimen measured 23.0 mm in length, 11.5 mm in height, and 11.0 mm in thickness. The original locality was unknown. P. ovata—Probably destroyed in World War II (Dance, 1986:210, 229). Not in MNH-U (R. Kilias, in correspondence, 20 January 1996). The original specimen measured 31 mm in length, 18 mm in height, and 16 mm in thickness. Perú. L. calderensis—Probably lost. Conrad did not provide a size or a figure. [?Puerto Caldera, Atacama Province (27.1°S)], Chile. P. rhyssodes-Not in the Museum at the Universidad de Chile, in Santiago, Chile (D. Frassinetti, in correspondence, 30 July 1996). The original specimen measured 48 mm in length, 25 mm in height, and 22 mm in thickness (Figure 30). Pleistocene and Recent material from Coquimbo, Coquimbo Province, Chile (30.0°S). The original figure is of a Recent specimen.

Description: Shell elongate, cylindrical; anterior end short, rounded; posterior end rounded to somewhat truncate, sometimes with an extension formed by outer layer of shell. Shell generally inflated, but large specimens sometimes flattened, moderately heavy to thin-shelled; beaks low. Without lunule or escutcheon. Sculpture of about 40 radial ribs that are moderate in strength and broad on anterior slope; ribs obscure on central slope, and about 10 very heavy, narrow radial ribs on posterior slope. Pallial sinus of moderate depth and width, rounded to somewhat pointed anteriorly, completely detached from pallial line; pallial line not bowed dorsally (Figure 63). Hinge teeth small; right valve with two produced cardinals, the posterior slightly bifid; left valve with two elongate cardinals, the anteriormost slightly bifid, lacking any sign of an anterior cardinal in the smallest specimens available. Ligament elongate, shallow, on a somewhat developed nymph. White to tan externally; white within. Length to 50 mm [SBMNH 125291; Lima, Lima Province, Perú].

Distribution and habitat: Lambayeque, Lambayeque Province, Perú (6.7° S) [one of the type localities of *P. tenuis*]; Viru, La Libertad Province, Perú (8.4° S) [SBMNH 138131], to Bahía Concepción, Concepción Province, Chile (37.1° S) [LACM 72–207.7]; Bahía de Lota, Concepción Province, Chile (37.1° S) (Soot-Ryen, 1959); the only habitat data recorded on labels is the in-

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Explanation of Figures 29 to 34

Figures 29–31. *Petricola (Petricolirus) rugosa* G. B. Sowerby I, 1834. Figure 29. *P. tenuis* G. B. Sowerby I, 1834; lectotype; BM(NH) 1995217/1; length, 26.0 mm. Figure 30. *P. rhyssoides* Philippi, 1887; original figure; original specimen length, 48 mm. Figure 31. BM(NH) 06.6.9.798; Coquimbo, Chile; length, 42.3 mm. Figures 32–34. *Petricola exarata* (Carpenter, 1857). Figure 32. *Rupellaria exarata*; lectotype; BM(NH) Carpenter Coll. 73(28); length, 4.7 mm; Figure 33. CAS 102591; Altata, Sinaloa, Mexico; length, 13.5 mm; Figure 34. CAS 102591; length, 4.0 mm; SEM image.

tertidal zone. Records in Chile from Archipelago de los Chonos, Aisen Province (approx. 44.5°S) (Soot-Ryen, 1959), and Bahía Orange, Isla Hoste, Magallanes Province (55.5°S) [USNM 17648], are doubtful and require additional verification; I have examined 37 Recent lots.

This species is recorded in the Pliocene of Chile (Herm, 1969:58).

Discussion: *Petricola tenuis* was based on thin-shelled specimens. This name was confused by Carpenter (1864a: 29 [1872:203], 1864b:552 [1872:33]) with *Saxicava tenuis* G. B. Sowerby I, 1834:88, in his discussions of the C. B. Adams collection, because Adams had specimens of a *Petricola* identified as the *Saxicava*.

This species is also highly variable in shape and sculpture, with some specimens almost cylindrical and others flattened and expanded. The sculpture varies from subdued to fairly heavy (Figure 30).

It seems possible that *P. costata* Philippi was based on material of this species (see Discussion under *P. denticulata*).

Based on the locality, it is likely that *Petricola chiloensis* Philippi, 1845, belongs in synonymy of *P. dactylus* (see under it). However, it is possible that subsequent records of Philippi's taxon, such as those of Hupé (1854), are based on specimens of *P. rugosa*.

It is with some hesitancy that I assign *P. ovata* to synonymy here. The original specimen had fewer ribs than does *P. olssoni*, which normally has 50–60 ribs. *Petricola rugosa* occasionally has a fairly oval shape, and can have as few as the 36 ribs counted by Troschel.

Conrad's "Laxicava" [Saxicava] calderensis is certainly this species. Many specimens of *P. rugosa* have a pattern of strong ribs on the ends, with the ribbing obsolete on the central slope. Given the species name, it seems likely that the original material came from Puerto Caldera, although Conrad did not supply a locality or a size, nor did he provide a figure.

Given the large size of the specimen and the figure, it is likely that *Petricola rhyssodes* belongs in synonymy here, and it is unfortunate that it has not been located among the Philippi material in the Museum at the Universidad de Chile.

Gray (1825:136) was the first to assign Gmelin *Mytilus niveus* Gmelin, 1791:3358, to the genus *Petricola*, and subsequent illustrations by G. B. Sowerby II seem to be the present species. Gmelin's taxon was based on the unavailable *Mytilus niveus* Chemnitz, 1785:154, pl. 82, fig. 734, reportedly from the Nicobar Islands in the Indian Ocean, and some material of *P. rugosa* in BM(NH) was subsequently labeled as having come from there. The figure in the non-binomial Chemitz, upon which Gmelin's species rests, is interminable, as is the description by Chemnitz: shell semi-transparent, edge knifelike, inner surface smooth and shiny, external surface with striae (not ribs).

Petricola, sensu lato

A variety of morphologies are represented by the following taxa, but with present knowledge, none can confidently be assigned to named subgenera.

Petricola exarata (Carpenter, 1857)

(Figures 32–34, 64)

Rupellaria exarata Carpenter, 1857. Carpenter, 1857b:244, 299, nomen nudum; Carpenter, 1857c:20–21; Lamy, 1923a:285; Coan, 1962:92; Brann, 1966:29, pl. 4, fig. 28; Keen, 1968:394, 395, fig. 16, 399 [Petricola (Petricola)]; Keen, 1971:197, 198, fig. 476 [Petricola (Petricola)]; Bernard, 1983:47 [Petricola (Petricola)].

Type material and locality: *R. exarata*—BM(NH) Carpenter Mazatlán Collection, Tablet 73, species 28, **lecto-type here designated**, paired valves; length, 4.7 mm; height, 3.0 mm; thickness, 1.6 mm (Figure 32). BM(NH), paralectotypes, two additional pairs, one in a barnacle. A fourth syntype mentioned by Carpenter & Keen (1968) not located. USNM 715645, paralectotypes, six fragmentary valves on a glass slide. Mazatlán, Sinaloa, Mexico (23.2°N); in barnacles attached to *Muricanthus princeps* (Broderip, 1833); F. Reigen.

Description: Shell ovate; anterior end very short, truncate to slightly rounded; posterior end rounded; posterior slope demarcated by a low keel. Young shells moderately inflated; adult generally flattened. Shell moderate in thickness; beaks very small. Lunule absent; long, narrow escutcheon in left valve. Sculpture of very fine, closely spaced radial threads (adult specimen with more than 100), slightly larger posteriorly, and irregular commarginal growth checks. Pallial sinus of moderate depth, broad, rounded, slightly overlapping pallial line; pallial line slightly bowed dorsally (Figure 64). Hinge teeth small; right valve with a small anterior cardinal and a bifid posterior cardinal, plus an elongate posterior lateral ridge; left valve with a very small anterior cardinal (lacking in many specimens), bifid central cardinal, and small posterior cardinal. Ligament of medium length, not sunken; nymph of moderate thickness. White externally, except for young portion of shell, which has broad brownish radial patches. Length to 15 mm [LACM 655645; Puerto Pizarro, Tumbes Province, Perú]. A photograph of large specimen (Figure 32) and an SEM view of a small specimen (Figure 34) are provided here.

Distribution and habitat: Altata, Sinaloa, Mexico (24.5°N) [CAS 102591, UCMP E8125], to Puerto Pizarro, Tumbes Province, Perú (3.5°S) [LACM 72–84.16; SBMNH 142893; USNM 655644, 655645], from the intertidal zone, nesting in crevices in rocky areas near muddy mangrove swamps and sand flats. I have examined 34 lots.

Discussion: This is a distinctive species with a number

of unique features. It is known mostly from very small specimens.

Petricola hertzana Coan, sp. nov.

(Figures 35, 36, 65)

- Petricola tellimyalis (Carpenter), auctt., non Psephis tellimyalis Carpenter, 1864. Dall, 1900a:100; Willett, 1931: 39, pl. 17, figs. 1, 2; Pilsbry & Lowe, 1932:96–97, pl. 13, figs. 12, 13; Burch, 1944:18–19; Burch, 1948:9–10; Bernard, 1983:57 [Petricola (Rupellaria)].
- [non Psephis tellimyalis Carpenter, 1864]. Carpenter, 1864b: 641 [1872:127]; Carpenter, 1865:135–136 [1872:303– 304]; Palmer, 1958:100–101, pl. 12, figs. 1–5.
- Petricola denticulata G. B. Sowerby I, auctt., non G. B. Sowerby I, 1843. Dall, 1900b:121–122 [in part].

Type material and locality: *P. hertzi*—CAS 104559, holotype, an articulated pair, length, 5.3 mm; height, 4.0 mm; thickness 2.8 mm (Figure 35). Paratypes, CAS 106035, 26 articulated and 5 disarticulated pairs, two of which are also figured here (CAS 104518) (Figure 36). San Pedro, Los Angeles County, California (33.7°N); on kelp.

Description: Shell ovate; anterior end shortest, sharply rounded; posterior end rounded. Shell inflated, thin; beaks broad. Without lunule or escutcheon. Sculpture primarily of irregular commarginal striae and low radial ribs, especially on ends; some specimens entirely lacking radial ribs, and some specimens with radial ribs over entire surface. Pallial sinus of moderate depth, broad, rounded, slightly confluent with pallial line; pallial sinus somewhat bowed dorsally (Figure 65). Hinge teeth relatively small, delicate, broken in most specimens; right valve with a narrow anterior cardinal and a slightly bifid posterior cardinal; left valve with a tiny anterior cardinal, a bifid central cardinal, and a narrow posterior cardinal. Ligament elongate, shallow, on a narrow nymph. Color variable, from cream to dark chocolate brown, in patches or radial bands; occasional specimens white. Length to 7 mm [CAS 106035, a paratype; San Pedro, Los Angeles County, California].

Distribution: Santa Monica, Los Angeles County, California (34.0°N) [ANSP 15759; CAS 104552, 104556, 104560; SBMNH 143007, 143008; LACM 19264, and other lots], to Bahía Magdalena, Baja California Sur (24.6°N) [ANSP 151718, SBMNH 15807], from the intertidal zone to 27 m, on algae. Two lots labeled as having come from Guaymas, Sonora, Mexico (27.9°N) [USNM 602882, UCMP A4200], both from old collections, may represent locality errors because no other material has come from that well-studied locality. However, the species should be looked for in that area because several other Californian species occur in isolated central Golfo de California populations. I have examined 55 lots.

This species has been reported, as *P. tellimyalis*, from the Pleistocene of southern California at Playa del Rey,

Los Angeles County (Willett, 1937:390), and Newport Bay, Orange County (Kanakoff & Emerson, 1959:24).

Etymology: This species is named in honor of Carole and Jules Hertz of San Diego, California.

Discussion and comparisons: Dall (1900a) was the first to identify this species of *Petricola* as *Psephis tellimyalis* Carpenter, which he presumed had been based on a very small specimen. This assignment is hard to explain because Carpenter specifically mentioned elongate lateral teeth, and the type was in the USNM. Dall (1900b) then became convinced that it was merely the young of *Petricola denticulata*. Willett (1931) eventually showed that it was a separable species, and Pilsbry & Lowe (1932) agreed, noting this as they reassigned southern Californian material that has been known as *P. denticulata* to their new species *P. californiensis*.

When I examined the tiny holotype of *Psephis tellimyalis* (length, 2.5 mm) [USNM 15554], I realized that it was not a *Petricola* at all, but rather a member of the Bernardinidae and a previously unrecognized synonym of *Halodakra* (*Halodakra*) subtrigona Carpenter, 1857:82 (this species discussed by Coan, 1984:231). This has left the small *Petricola* without a name.

Petricola olssoni Bernard, 1983

(Figures 37, 38, 66)

- Petricola (Petricola) peruviana Olsson, 1961, non (Jay, 1839). Olsson, 1961:315, pl. 55, fig. 9; Keen, 1971:199, 200, fig. 482 [as Petricola (Rupellaria)].
- [non Venerupis peruviana Jay, 1839, a synonym of P. denticulata]
- Petricola olssoni Bernard, 1983, nom. nov. pro P. peruviana Olsson, non (Jay, 1839). Bernard, 1983:57, 70 [Petricola (Rupellaria)].
- Petricola rugosa G. B. Sowerby I, 1834, auctt., non G. B. Sowerby I, 1834. Marincovich, 1973: fig. 18.

Type material and locality: *P. peruviana* Olsson/olssoni—ANSP 218905, a right valve; length, 30.0 mm; height, 19.0 mm; thickness, 5.6 mm (Figure 37). Negritos, Piura Province, Perú (4.7°S). ANSP 218906, paratype, a left valve, 30.0 mm in length, from Lobitos, Piura Province, Perú (4.4°S) (Figure 38).

Description: Shell ovate; anterior end shortest, rounded; posterior end broadly expanded, rounded to slightly truncate. Small specimens moderately inflated; larger material sometimes flattened. Shell inflated, thin; beaks prominent. Without lunule or escutcheon. Sculpture of about 50–60 fine, narrow radial ribs over entire surface, ribs varying somewhat in width, becoming somewhat less conspicuous posteriorly, and strong, irregular commaringal growth checks. Pallial sinus of moderate depth and width, pointing somewhat anterodorsally, rounded, overlapping pallial line for a substantial distance; pallial line greatly bowed dorsally, often broken into irregular patches (Fig-



ure 66). Hinge teeth relatively small; right valve with a narrow anterior cardinal and a produced, slightly bifid posterior cardinal; left valve with a tiny anterior cardinal, a slightly bifid central cardinal, and a thin posterior cardinal. Ligament elongate, shallow; nymph fairly robust. White to tan externally, often with wide radial brownish bands; internally mottled with orange-brown. Length to 30 mm (type material of *P. peruviana* Olsson). A complete pair is also illustrated here (Figure 39).

Distribution and habitat: Between Zorritos and Mancora, Tumbes Province, Peru (3.9°S) [SBMNH 125769], to Antofagasta, Antofagasta Province, Chile (23.7°S) [LACM 54743], from the intertidal zone to 3 m, in nest-ling situations. I have examined 22 lots.

Discussion: This species is most similar to *P. californiensis*, which attains a larger size, is more elongate and proportionately longer posteriorly, and has heavier sculpture in general, particularly anteriorly.

Petricola scotti Coan, sp. nov.

(Figures 40, 41, 67)

Petricola (Naranio) sp., auctt. Olsson, 1961: 528, pl. 55, fig. 11 [plate expl. makes reference to p. 317, but species not mentioned there].

Type material and locality: *P. scotti*—PRI 25782, holotype, paired valves; length, 16.9 mm; height, 8.6 mm; thickness, 7.2 mm (Figure 40). Esmeraldas, Guayas Province, Ecuador (1.0°N); habitat not recorded; A. A. Olsson. CAS 102509, paratype, paired valves; length, 11.0 mm (Figure 41); Manta, Manabi Province, Ecuador (1.0°S); Don L. Frizzell

Description: Shell ovate-elongate; anterior end very short, rounded to subtruncate; posterior end rounded, extended beyond inner shell layer by outer shell layer in some specimens; posterodorsal margin somewhat flared, with right valve overlapping left. Shell inflated, average in thickness; beaks slightly inflated. Lunule absent; small escutcheon posterior to ligament in some material. Sculpture on initial portion of shell of approximately 50 radial ribs, becoming somewhat finer posteriorly; at approximately 6 mm in size, sculpture transitioning entirely to thin, evenly spaced commarginal lamellae, which can be as high as their interspaces. Pallial sinus of moderate depth and width, rounded anteriorly, overlapping or very

closely paralleling pallial line for a short distance; pallial line slightly bowed dorsally (Figure 67). Hinge fairly robust; right valve with a projecting anterior cardinal and a bifid posterior cardinal; left valve with a very low, inconspicuous anterior cardinal, a bifid central cardinal, and a thin, elongate posterior cardinal. Ligament short, shallow. Shell white externally and internally. Length to 18.5 mm [MNHN; La Puntilla, Guayas Province, Ecuador].

Distribution and habitat: Ft. Amador, Panamá Province, Panamá (9.0°N) [SBMNH 142891], to Salinas, Guayas Province, Ecuador (2.2°S)[USNM 635362]; the only habitat noted was in algae. This species is as yet known from 9 lots.

Referred material: Skoglund Collection—Venado Beach, Panamá Province, Panamá (8.9°N); LACM 75-56.19—Playa de Farfan, Panamá Province, Panamá (8.9°N); LACM 65461—Ft. Amador, Panamá Province, Panamá (9.0°N); SBMNH 142891—Ft. Amador, Panamá Province, Panamá (9.0°N); PRI 25782—Esmeraldas, Guayas Province, Ecuador (1.0°N)—Holotype; CAS 102509—Manta, Manabi Province, Ecuador (1.0°S)— Paratype; NMNH—La Puntilla, Guayas Province, Ecuador (2.2°S); NMHN—Peninsula Santa Elena, Guayas Province, Ecuador (2.2°S); USNM 635326—Salinas, Guayas Province, Ecuador (2.2°S).

Etymology: This species is named for Paul H. Scott of the Santa Barbara Museum of Natural History.

Discussion: I initially mistook specimens of this species for *Petricola concinna*, from which it differs in being more ovate and less tapered posteriorly, in having even radial sculpture on the early portion of the shell rather than a few radial ribs concentrated anteriorly, and in having a pallial sinus that overlaps the pallial line for a short distance. Two of the four lots from Panama include some very tiny specimens that can only be tenatively assigned here. This species differs from young *P. denticulata* in having a more rounded outline, with a less produced anterior end, in developing frills on the posterior slope, and in having lower radial sculpture.

Genus Choristodon Jonas, 1844

Choristodon Jonas, 1844:185 [Type species (M): C. typicum Jonas, 1844:185, =Petricola robusta G. B. Sowerby I, 1834:47; Recent, Caribbean and eastern Pacific].

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Explanation of Figures 35 to 41

Figures 35, 36. *Petricola hertzana* Coan, sp. nov. Figure 35. Holotype; CAS 104559; length, 5.3 mm. Figure 36a, b. Paratypes; CAS 104518; same magnification. Figures 37–39. *Petricola olssoni* Bernard, 1983. Figure 37. Holotype; ANSP 218905; length, 30.0 mm. Figure 38. Paratype; ANSP 218906; length, 30.0 mm. Figure 39. SBMNH 126151; Pisco, Ica Province, Peru; length, 12.0 mm. Figures 40, 41. *Petricola scotti* Coan, sp. nov. Figure 40. Holotype; PRI 25782; length, 16.9 mm. Figure 41. Paratype; CAS 102509; length, 11.0 mm.



This genus is characterized by a heavy shell, heavy radial sculpture, a sunken ligament, a hinge that becomes distorted in large specimens, and a tendency to become inequivalve, the right valve overlapping the left posterodorsally. It was synonymized with the Mediterranean Rupellaria by Keen (1969); the latter genus is thin-shelled and equivalve, has fine radial ribs, and the ligament is not deeply sunken. Moreover, the foot is elongate in *Petricola (Rupellaria) lithophaga* (Retzius, 1788), as are the siphons, and the pallial sinus is very large (Deshayes, 1848:Atlas, pp. 139–145, pls. 66, 67, 67a). In contrast, *Choristodon robustum* has a small foot, short siphons, and a smaller pallial sinus (Narchi, 1974).

Choristodon robustum (G. B. Sowerby I, 1834)

(Figures 42–48, 68)

- Petricola robusta G. B. Sowerby I, 1834. G. B. Sowerby I, 1834:47; Deshayes, 1853:210-211; G. B. Sowerby II, 1854b:775, pl. 166, figs. 16, 17; Gould & Carpenter, 1857:198; Carpenter, 1857b:184, 226, 232, 234, 244, 265, 295, 299, 352, 364, 365; Fischer, 1857:323, 325, 327-329; Carpenter, 1857c:17-19, 547; Carpenter, 1864b:529, 543, 620 [1872:15, 29, 106]; Tryon, 1872: 257, 258 [as a synonym of P. lithophaga (Retzius, 1788)]; G. B. Sowerby II, 1874a:pl. 3, fig. 30; Dall, 1909b:270; Lamy, 1923b:330-332; Hertlein & Strong, 1948:194 [Petricola (Petricola)]; Durham, 1950:87, 168, pl. 23, fig. 15; Keen, 1958:152, 153, fig. 349 [Petricola (Rupellaria)]; Olsson, 1961:215 [Petricola (Petricola)]; Emerson & Hertlein, 1964:359; Brann, 1966: pl. 2, fig. 24; Keen, 1971:199, 200, fig. 483 [Petricola (Rupellaria)]; Woodring, 1982:709 [as a synonym of P. typica Jonas, 1844].
- Choristodon typicum Jonas, 1844. Jonas, 1844:185; Jonas, 1846:101–103, 133 [repr:1–3, 33], pl. 7, fig. 3, 3a, 3b; [the following references mostly as *Petricola*]; Deshayes, 1853:510; G. B. Sowerby II, 1874a:pl. 3, fig. 21; Carpenter, 1857b:244, 364 [as a probable synonym of *P. robusta*]; Fischer, 1857c:19, 529, 547 [as a probable synonym of *P. robusta*]; Carpenter, 1857c:19, 529, 547 [as a probable synonym of *P. robusta*]; Carpenter, 1864b:543 [1872: 29]; Tryon, 1872:257, 258 [as a synonym of *P. lithophaga*]; Dall, 1900c:1059; Lamy, 1923b:332–333; Weisbord, 1964:329–332, pl. 47, fig. 15, pl. 48, figs. 1–6 [*Petricola (Rupellaria*]; Narchi, 1974:123–129; Woodring, 1982:709–710, pl. 118, fig. 2 [*Rupellaria*]; Rios, 1994:290, pl. 99, fig. 1419.
- Petricola robusta Philippi, 1849 (March) [non P. robusta G. B. Sowerby I, 1834]. Philippi, 1849:163; Carpenter,

1857b:295 [as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Carpenter, 1857c:17 [as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Tryon, 1872:257, 258 [as a synonym of *P. lithophaga*].

- Petricola sinuosa Conrad, 1849 (pre-16 June). Conrad, 1849a:155; 1849c:229; 1850:279, pl. 39, fig. 2; [the following three references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Carpenter, 1857a:209; Carpenter, 1857b:226, 244, 265; Carpenter, 1857c:547; Tryon, 1872:257, 258 [as a synonym of *P. litliophaga*]; [the following five references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Lamy, 1923b:331; Hertlein & Strong, 1948:194; Keen, 1958:152; Keen, 1971:199; Bernard, 1983:57.
- Petricola bulbosa Gould, 1851. Gould, 1851:16, 408, pl. 15, fig. 5; [the following four references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Gould & Carpenter, 1857:198; Carpenter, 1857b:226, 232, 244; Carpenter, 1857c:547; Gould, 1862:210; Tryon, 1872:255, 257 [as a synonym of *P. lithophaga*]; [the following six references as a synonym of *P. robusta* G. B. Sowerby I, 1834]; Lamy, 1923b:331; Hertlein & Strong, 1948:194; Keen, 1958:152; R. I. Johnson, 1964:48; Keen, 1971: 199; Bernard, 1983:57.
- Petricola anchoreta de Folin, 1867. de Folin, 1867:56–58
 [repr.:18–20], pl. 3, figs. 1–4; de Folin & Périer, 1867:
 8; Tryon, 1872:255; Lamy, 1923b:320; Kisch, 1960:
 162; Bernard, 1983:57 [as a synonym of *P. exarata*].
- *Petricola venusta* de Folin, 1867. de Folin, 1867:58–59 [repr.:20–21], pl. 3, figs. 5–7; de Folin & Périer, 1867: 8; Tryon, 1872:258; Kisch, 1960:162.
- *Petricola buwaldi* Clark, 1915. Clark, 1915:471, pl. 60, fig. 6; Adegoke, 1969:149; ?Woodring & Bramlette, 1951: 66, 90.
- Petricola (Rupellaria) riocanensis Maury, 1917. Maury, 1917:384 [220], 414 [250], pl. 37, fig. 12; Woodring, 1982:709 [as a synonym of P. typica].

Type material and localities: *P. robusta* G. B. Sowerby I—BM(NH) 1966558/1, **lectotype here designated**, paired valves; length, 30.6 mm; height, 24.4 mm; thickness, 21.2 mm (Figure 42). BM(NH) 1966558/2-3, paralectotypes, two additional pairs, 26.2 mm and 21.5 mm in length. Panamá and "Isla Muerto" [?Isla Santa Clara], Golfo de Guayaquil, El Oro Province, Ecuador (3.2°S). The label now with the specimens says: "Panamá, found in rocks at 6–11 fms." [11–20 m]. *C. typicum*—Probably lost. Not in MNH-U (R. Kilias, in correspondence, 20 January 1996). The original specimen measured 16.5 mm in length, 11.0 mm in height, and 8.8 mm in thickness (Figure 43). St. Thomas, Virgin Islands (about 18.3°N).

Explanation of Figures 42 to 48

Figures 42–48. *Choristodon robustum* (G. B. Sowerby I, 1834). Figure 42. *Petricola robusta*; lectotype; BM(NH) 1966558/1; length, 24.4 mm. Figure 43. *Choristodon typicum* Jonas, 1844; figure from Jonas (1846); length, 16.5 mm. Figure 44. *Petricola sinuosa* Conrad, 1849; as figured in Conrad (1850); length, 19 mm. Figure 45. *P. bulbosa* Gould, 1851; holotype; MCZ 169065; length, 27.8 mm. Figure 46. *P. anchoreta* de Folin, 1867; lectotype; BM(NH) 1995222/1; length, 12.4 mm. Figure 47. *P. venusta* de Folin, 1867; holotype; BM(NH) 1995223/1; length, 16.3 mm. Figure 48. *P. buwaldi* Clark, 1915; holotype; UCMP 11657; length, 29.5 mm.

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P. robusta Philippi-Probably lost. Not in MNH-U (R. Kilias, in correspondence, 20 January 1996). The original specimen measured 15.4 mm in length, 14.3 mm in height, and 12.1 mm in thickness. Panamá, in association with the pearl oyster "Avicula margaritifera" [= Pinctada mazatlanica (Hanley, 1856)]. P. sinuosa-Probably lost. The original specimen measured 19 mm in length, 15 mm in height, and 14 mm in thickness (Figure 44). Either Baja California or Peru. P. bulbosa-MCZ 169065, holotype, paired valves; length, 27.8 mm; height, 22.2 mm, thickness, 17.4 mm (Figure 45). Guaymas, Sonora, Mexico (27.9°N); T. P. Green. P. anchoreta-BM(NH) 1995222/1, lectotype here designated, paired valves; length, 12.4 mm; height, 10.8 mm; thickness 8.2 mm (Figure 46). BM(NH) 1995222/2-5, paralectotypes, one pair of 20 mm in length, and three valves, 8.8 mm, 7.0 mm, and 3.6 mm in length. Archipelago de las Perlas, Panamá (approximately 8.4°N). The lectotype selected is the specimen closest to de Folin's figures 1 and 2 and is reasonably close to his stated measurements. P. venusta-BM(NH) 1995223/1, lectotype here designated, left valve; length, 16.3 mm; height, 15.2 mm; thickness, 4.8 mm (Figure 47). BM(NH) 1995223/2-3, paralectotypes, one pair of 11.2 mm and a left valve of 15.6 mm in length. Archipelago de las Perlas, Panamá (approximately 8.4°N). Because none of the specimens is a close match for de Folin's figure or measurements, the largest specimen was selected as lectotype. P. buwaldi-UCMP 11657, holotype, left valve [mislabeled as right on plate explanation]; length, 29.5 mm; height, 25.0 mm; thickness, 10.5 mm (Figure 48). Southeast of Walnut Creek, Contra Costa County, California (37.9°N); Upper San Pablo Group; Upper Miocene; UC Locality 1942 [not in locality list in Clark, 1915:505-512]. P. riocanensis-PRI 42067 [not examined], holotype, right valve; length, 21 mm; height, 17 mm; thickness, 8 mm. Río Cana, Caimito, Dominican Republic; Miocene.

Description: Shell ovate to ovate-trigonal; anterior end short, rounded; posterior end often produced, broadly to narrowly truncate; right valve sometimes overgrowing left valve especially posterodorsally. Shell inflated, moderately thick; beaks prominent. Without lunule or escutcheon. Sculpture of about 50 narrow, heavy radial ribs that are lowest and most dense anteriorly and heaviest and most widely spaced posteriorly, and fine commarginal threads. Ribs scalloping posterior margin. Pallial sinus of moderate depth, broad, rounded anteriorly, not confluent with pallial line; pallial line not bowed dorsally (Figure 68). Hinge teeth very robust, often becoming gerontic in adult; right valve with a produced anterior cardinal and an elongate, slightly bifid posterior cardinal; left valve with a very small anterior cardinal, which is obliterated in adult, a narrow, slightly bifid central cardinal, and an elongate posterior cardinal. As first pointed out by Fischer (1857:323), with a tendency for the teeth of one valve to fuse into those of the opposite valve, and, when the valves are separated, to break off and either remain embeded there or to become detached and lost. Ligament short, on a heavy nymph, deeply sunken. White to tan externally; reddish purple to dark purple within, especially posteriorly. Length to 42.5 mm [Skoglund Collection; Guaymas, Sonora, Mexico].

Distribution and habitat: Laguna Ojo de Liebre [Scammons], Baja California Sur (27.8°N) [ANSP 263845; SDNHM 29611], into the Golfo de California as far north as Puerto Peñasco, Sonora (31.3°N) [SBMNH 32484 and other lots; CAS 102500], Mexico, to Panamá (approximately 9°N) [CAS 105778; USNM 22832, 105228, 131808, 620701], and south to Paita, Piura Province, Peru (5.1°S) [MNHN], and and Isla Baltra, Islas Galápagos, Ecuador (0.4°S) [MNHN]; in the western Atlantic from North Carolina [USNM 602882] to Rio Grande do Sol, Brazil (Narchi, 1974), from the intertidal zone to 55 m, in calcareous substrata, such as shells of *Spondylus*, colonial corals, and calcareous bryozoans, as well as in colonies of polychaetes made of agglutinated sand. I have examined 82 Recent eastern Pacific lots.

Recorded from the Pleistocene of Bahía Magdalena, Baja California Sur (Jordan, 1936:112); Isla Coronados (Durham, 1950:87, Emerson & Hertlein, 1964:349, 359) and Isla San Marcos (Durham, 1950:87), in the Golfo de California; and Ecuador (Hoffstetter, 1948:78; MNHN). Occurring in the Late Miocene of northern California (type of *P. buwaldi*), central California (Gale, in Preston, 1931:15; Woodring & Bramlette, 1951:66, 90; Adegoke, 1969:149), the Dominican Republic (type of *P. riocanensis*), and Panama (Woodring, 1982:709–710). Also in the Pliocene and Pleistocene of Venezuela (Weisbord, 1964: 331) and the Pliocene of Florida (Dall, 1900c:1059).

Discussion: Carpenter (1857c) was the first to conclude that *P. robusta* Philippi, 1849, was not only a homonym but also a synonym of *P. robusta* G. B. Sowerby I, 1834. Perhaps Philippi had in hand a specimen labeled *robusta* and thought it was only a manuscript name.

It has long been recognized that C. robusta is very similar to the Caribbean C. typica Jonas, 1844, type species of Choristodon. Carpenter (1857c:19) thought they might be synonyms, and Woodring (1982:709) synonymized them (unfortunately placing the senior P. robusta into the synonymy of the younger P. typica). Some possible morphological differences were noted and should be made the subject of statistical study of their significance: eastern Pacific material may attain a larger size, may be more produced and attenuate posteriorly, may have heavier ribs, and its internal color may tend to be purplishbrown, whereas Caribbean material seems to be greenish or brownish-green within. On the other hand, Weisbord's (1964) contention that P. robusta has a shorter pallial sinus than Caribbean material does not seem to be true. However, in the course of the present study, insufficient material from both coasts was available simultaneously to test these differences, and they have been left in synonymy pending future, more detailed study by other workers.

Although the type specimen of *P. sinuosa* Conrad is missing, its illustration in Conrad (1850) makes clear that it is a synonym, and the type specimen of *P. bulbosa* proves that it is as well. Both have relegated to synonymy since Carpenter (1857c).

The type specimens of *Petricola anchoreta* and *P. ven-usta*, both deFolin, 1867, thought to have been lost (Kisch, 1960), have been located and are both based on small specimens of this species.

Woodring (1982) placed *Petricola (Rupellaria) riocanensis* Maury, 1917, from the Miocene of Dominican Republic, into the synonymy of *P. typica*, and also reported the species from the Miocene of Panamá. Examination of the type specimen of *P. buwaldi*, as well as the specimen cited by Adegoke (1969), demonstrates that this material is within the range of variability of the Recent species. A detailed study of Recent material from both coasts should take this sparse fossil material into account as well.

Records of this species from South Africa, both as *P. robusta* and as *P. typica* (for example, G. B. Sowerby III, 1890:157, 1892:60, 61, 1897:33; Smith, 1906:65; Turton, 1932:246), were based on specimens *Petricola bicolor* G. B. Sowerby II, 1854b:776, pl. 166, fig. 22 (Barnard, 1964:513). This species has a much thinner shell, finer sculpture, and a less robust hinge.

Fischer (1857) noted that *Choristodon robustum* has elongate siphons, a very small foot, very unequal ctenidia, and very small labial palps. Narchi (1974) described the functional morphology of *Choristodon robusta* [as "*Petricola (Rupellaria) typica*"]. Its burrows in calcaleous substrata are shallow, oval, and presumably enlarged by mechanical rasping. The siphons are short, subequal, and fused for half their length. The inhalent siphon is fringed by large pinnate tentacles of two sizes plus two ranks of simple tentacles. The exhalent siphon has smaller, less complex tentacles and a terminal valvular membrane. The ctenidia have 14–18 shallow plicae. The outer demibranch is only about half the size of the inner. The labial palps are small and triangular. The foot is small.

Genus Petricolaria Stoliczka, 1870

Petricolaria Stoliczka, 1870:139–140 [Type species: *Petricola pholadiformis* Lamarck, 1818:505; subsequent designation of Stoliczka, 1871:xvii]

Stoliczka's text included two species within his new genus and no type designation, the later-published table at the front of his book, which is headed "Synoptical list of the families and genera noticed in the present volume, together with the respective type-species," constitutes a subsequent designation. Members of this genus are elongate, thin shelled, with strong, scaly radial ribs on the anterior end and radial threads posteriorly. The hinge is thin and delicate.

Petricolaria cognata (C. B. Adams, 1852)

(Figures 49, 50, 69)

- Petricola cognata C. B. Adams, 1852. C. B. Adams, 1852a: 510–511, 546–547 [1852b:286–287, 322–323]; Carpenter, 1857b:279, 299, 363; Carpenter, 1864a:29 [1872: 203] [as a possible synonym of *P. pholadiformis*]; Carpenter, 1864b:552 [1872:38] [as a possible synonym of *P. pholadiformis*]; Tryon, 1872:256; Arnold, 1903:156; Lamy, 1923b:347 [as a synonym of *P. pholadiformis*]; Grant & Gale, 1931:356 [as a synonym of *P. pholadiformis*]; Grant & Gale, 1931:356 [as a synonym of *P. pholadiformis*]; Turner, 1956:38, 130, pl. 19, figs. 3, 4; Soot-Ryen, 1957:9; Keen, 1958:152, 153, fig. 346; Olsson, 1961: 316, pl. 54, figs. 5, 5a; Keen, 1971:197, 198, fig. 478.
- Petricola gracilis parallela Pilsbry & Lowe, 1932. Pilsbry & Lowe, 1932:99–100, pl. 13, figs. 4, 5, 5a, 6; [the following five references as *Petricola parallela*]; Hertlein & Strong, 1948:195; Keen, 1958:152, 153, fig. 348; Olsson, 1961:315–316, pl. 54, figs. 3–3b; E. J. Moore, 1968:66–67, pl. 31, fig. e; Keen, 1971:198, 199, fig. 480; Bernard, 1983:57 [as a synonym of *P. gracilis*]; Avilés & Sánchez, 1983:102, fig. 2.
- Petricola gracilis Deshayes, auctt., non Deshayes, 1853. Bernard, 1983:57 [Petricola (Petricolaria)].
- [non Petricola gracilis Deshayes, 1853]. Deshayes, 1853:
 214; Deshayes, 1854:pl. 18, fig. 6; G. B. Sowerby II, 1854b:772, pl. 164, fig. 12.
- P. pholadiformis Lamarck, auctt. non Lamarck, 1818. Carpenter, 1864b:537 [1872:23]; Grant & Gale, 1931:356 [in part].

Type material and localities: *P. cognata*—MCZ 186308, holotype, paired valves, the right substantially broken, the left chipped posteriorly; length, 22.3 mm; height, 10.2 mm; thickness, 5.4 mm (Figure 49). Panamá, presumably near Ciudad de Panamá (9.0°N); C. B. Adams, 27 November 1850–2 January 1851. *P. gracilis parallela*—ANSP 155591, holotype, formerly filed in SDNHM 50799 as "paratype"; length, 28.7 mm; height, 10.2 mm; thickness, 9.6 mm (Figure 50); ANSP 398891, paratypes, three left valves measuring 43.5 mm, 31.6 mm, and 26.9 mm in length; the first was illustrated in Pilsbry & Lowe (1932:pl. 13, fig. 6). Corinto, Chinandega Province, Nicaragua (12.5°N); H. N. Lowe.

Description: Shell elongate to very elongate, cylindrical; anterior end very short, somewhat pointed; posterior end elongate, rounded to truncate, somewhat laterally flattened in large specimens. Shell inflated, thin; beaks small. With a lunule demarcated by anteriormost radial rib and lacking prominent sculpture; without escutcheon. Anterior end with about eight heavy, well-spaced radial ribs; ribs with nodes dorsally and produced, ventrally curved scales toward anteroventral margin; central and posterior slopes with approximately 20 thin radial threads. Hinge



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teeth small; right valve with a small anterior cardinal and a bifid posterior cardinal; left valve with a small anterior cardinal, a bifid central cardinal, and an elongate posterior cardinal. Pallial sinus deep, narrow, pointed anteriorly, paralleling but completely detached from pallial line; pallial line not bowed dorsally (Figure 69). Ligament relatively short, not sunken; nymph thin. External and internal color white, stained with brown posteriorly. Length to 80 mm [CAS 105784; Laguna Ojo de Liebre, Baja California Sur].

Distribution and habitat: Isla Cedros, Baja California [Norte] (28.4°N) [LACM 72–113], and Laguna Ojo de Liebre [Scammon], Baja California Sur (27.9°N) [CAS 105784; LACM 72–1.1], to and throughout the Golfo de California to Puerto Peñasco, Sonora (31.3°N) [SBMNH 124920], Mexico, and south to Isla Puná, Golfo de Guayaquil, Guayas Province, Ecuador (2.8°S) [CAS 105785; MNHN], from the intertidal zone to 15 m, in soft substrata, such as clay banks. I have examined 91 lots. Dall (1900b:122) cited San Diego, California, as a locality, but no specimens have been located from there.

This species is also present in the Pleistocene of southern California (San Pedro—Arnold, 1903:156; Valentine & Meade, 1961:8, 24; Huntington Beach—Valentine (1959:53, 54); Newport Bay—Bruff, 1946:232; Kanakoff & Emerson, 1959:24, 35; Valentine & Meade, 1961:24, 28; and San Diego—Dall, 1878a:11; 1878b:28; Kanakoff, in Emerson & Chace, 1959:338, 341; E. J. Moore, 1968: 66).

Discussion: The holotype of *P. cognata* is a short, thick but not highly unusual specimen (for example, USNM 153348, also from Panamá). Insufficient material was available in 1932 when Pilsbry & Lowe described *P. gracilis parallela*.

Pilsbry & Lowe (1932) appropriately recognized the similarily of their new species to *P. gracilis* Deshayes, 1853. Described from an unknown locality, *P. gracilis* has subsequently been recognized from the Indian Ocean and the Red Sea (Oliver, 1992: 194, pl. 44, fig. 7). The syntypes of this species are extant [BM(NH) 196953]. It differs in having (1) a less produced anterior end, (2) denser sculpture on the anterior end, (3) sharper, narrower scales on the radial ribs near its anteroventral margin, and (4) a less demarcated lunule.

Two other tropical members of this genus have been

described, but their relationships to P. gracilis have yet to be resolved. The first is Petricolaria serrata (Deshayes, 1853), described in error from New Zealand (Deshayes, 1853:212, 1854:pl. 18, fig. 11), where petricolids are as yet unknown (Powell, 1979). It matches material I have seen from West Africa that has a very rugose anterior end, with very broad scales, and that lacks a lunule. However, it may be a synonym of P. gracilis. The second is P. stellae Narchi, 1975, occurring from Brazil to Uruguay; its anterior end is, in general, less produced and more densely sculptured than P. cognata. Its scales are also broader than those of P. cognata, and there is no demarcated lunule, with heavy commarginal ribs running onto the anterodorsal slope. It also has a poorly developed anterior cardinal in the left valve; there may also be some other subtle differences in dentition among these taxa, as discussed by Narchi (1975); the source of his specimens of "P. pholadiformis gracilis" is not made clear. In any event, these tropical species account for all records of the Northern Hemisphere Petricolaria pholadiformis in the Southern Hemisphere.

For comparisons with *P. pholadiformis*, see under next species.

Narchi (1975) described the anatomy of *Petricolaria stellae*, which forms burrows in polychaete worm colonies, a fairly hard substratum, by valve abrasion. The siphons are fused for half of their length and can be extended to a distance equal to the shell length. The inhalent siphon has four ranks of tentacles, the inner dentritic, the second and third pinnate, and the outermost simple. The exhalent siphon has three ranks of tentacles, the innermost pinnate, the outer two simple, and an rudimentary terminal valvular membrane. The outer demibranch is smaller than the inner, does not extend as far forward, and has a dorsal supra-axial extension. Each demibranch has 10–13 folds, with an average of 12 filaments per fold. The labial palps are small and triangular, and the coil and uncoil actively.

Petricolaria pholadiformis (Lamarck, 1818)

(Figures 51-53, 70)

Petricola pholadiformis Lamarck, 1818. Lamarck, 1818: 505; G. B. Sowerby I, 1823:figs. 1, 2; Conrad, 1832: 37, pl. 7, fig. 3; Say, 1834:[2 pp.], pl. 60, fig. 1; De Kay, 1844:228, pl. 28, fig. 282; Deshayes, 1853:211–

Explanation of Figures 49 to 54

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Figures 49, 50. *Petricolaria cognata* (C. B. Adams, 1852). Figure 49. *Petricola cognata*; holotype; MCZ 186308; length, 22.3 mm. Figure 50. *P. gracilis parallela* Pilsbry & Lowe, 1932; holotype; ANSP 155591; length, 28.7 mm. Figures 51–53. *Petricolaria pholadiformis* Lamarck, 1818. Figure 51. *Petricola pholadiformis*; holotype; MHNG; length, 46.0 mm. Figure 52. *Gastranella tumida* Verrill, 1872; lectotype; PMYU 8845a; length, 2.2 mm. Figure 53. *Petricolaria pholadiformis* lata Dall, 1925; lectotype; USNM 95645; length, 53.4 mm. Figure 54. *Thracia curia* Conrad, 1837. *Ungulina luticola* Valenciennes, 1846; lectotype; MNHN; length, 10.4 mm.

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212; G. B. Sowerby II, 1854b:771, pl. 166, fig. 1; Tuomey & Holmes, 1856:87–88, pl. 21, fig. 5; Gould, 1870: 90–92, figs. 398, 399; Tryon, 1872:257; G. B. Sowerby II, 1874a:pl. 1, fig. 7; Dall, 1889:58–59, pl. 59, fig. 15, pl. 64, fig. 140a; Dall, 1900c:1061; Lamy, 1921:435– 436; Lamy, 1923b:342–344; Grant & Gale, 1931:356 [in part]; Jacobson, 1943:142; Burch, 1944:18; Hanna, 1966:60, fig. 69; Bernard, 1983:57, 70 [*Petricola (Petricolaria)*]; Campbell, 1993:46, pl. 20, fig. 181 [pp. 212–213]; Poppe & Goto, 1993:127, pl. 23, fig. 6.

- Petricola fornicata Say, 1822. Say, 1822:319–320; Conrad, 1832:37 [as a synonym of P. pholadiformis]; Deshayes, 1853:212; Tryon, 1872:257 [as a synonym of P. pholadiformis].
- Petricola flagellata Say, 1834. Say, 1834:[1 p.] [in synonymy of *P. dactylus* G. B. Sowerby 1, of Say].
- *Petricola carolinensis* Conrad, 1863. Conrad, 1863:576; Dall, 1900c:1060; Campbell, 1993:46 [as a synonym of *P. pholadiformis*].
- *Gastranella tumida* Verrill, 1872. Verrill, 1872:211, 286, pl. 6, figs. 3, 3a; Verrill, 1873:678–679, pl. 26, fig. 190; Verrill, 1882:568; Dall, 1900c:1061 [as a synonym of *P. pholadiformis*]; R. I. Johnson, 1989:71.

Petricolaria pholadiformis lata Dall, 1925. Dall, 1925:90.

- Petricola rogersi McGavock, 1944. McGavock, 1944:2; Campbell, 1993:46 [as a synonym of *P. pholadiformis*].
- Petricola dactylus G. B. Sowerby I, acutt, non G. B. Sowerby 1, 1823. Say, 1834:[1 p.], pl. 60, fig. 2; De Kay, 1844:228–229, pl. 28, fig. 283; Gould, 1870:92–93; Dall, 1889:58 [as a variety of *P. pholadiformis*]; Dall, 1900c:1061 [as a separable species]; C. W. Johnson, 1914:95; Lamy, 1923b:345–346 [in part].
- [*non Petricola dactulus* G. B. Sowerby I, 1823:*Petricola* sp. 3; see under this species above]

Type material and localities: *P. pholadiformis*—MHNG 1082/97, holotype, paired valves; length, 46.0 mm; height, approx. 16 mm; thickness [measurement not obtained] (Figure 51). Original locality unknown; the type locality is here clarified to be Massachusetts, USA. *P.*

fornicata-Lost. The original dimensions were: height, 43 mm; width, 15 mm; thickness, 23 mm. [east coast] of North America. P. carolinensis-Possibly in AMNH (L. Campbell, in correspondence, 2 February 1996). Not listed in Moore (1962). Based on the material discussed and illustrated by Tuomey & Holmes (1856:87-88, pl. 21, fig. 5) as P. pholadiformis, from Pee Dee River [Raysor Marl] and Smith, Goose Creek [lower Waccamaw Formation], South Carolina; Pliocene. G. tumida-PMYU 8845a, lectotype here designated, a right valve (with broken hinge), glued in a mount, formerly part of a set of paired valves; the left valve has been lost; length, approx. 4 mm; height, approx. 2.2 mm; thickness could not be measured (Figure 52). PMYU 1845b, paralectotypes, two smaller, sealed pairs glued in the same mount. Long Island Sound near New Haven, New Haven County, Connecticut. Label adds: "off South End [Point], 4-6 fms. [7-11 m]; A. E. Verrill" (41°N). P. pholadiformis lata-USNM 95645, lectotype here designated, paired valves; length, 53.4 mm; height, 26.5 mm; thickness, 19.0 mm (Figure 53). The lectotype selected is the largest specimen in the lot. USNM 880151, paralectotypes, 3 pairs (48.8 mm, 45.1 mm, 36.0 mm in length), one left valve (52.6 mm in length). Quahog Bay, Cumberland County, Maine (43.8°N). P. rogersi-ANSP 16015, syntypes [not studied]. Yorktown, Virginia (37.2°N); "Yorktown formation; Pliocene," but more likely late Pleistocene [L. Campbell, in correspondence, 2 February 1996].

Description: Shell elongate, cylindrical; anterior end very short, sharply rounded; posterior end elongate, broadly rounded. Shell inflated, thin; beaks small. Without lunule; anterodorsal slope with commarginal sculpture; without escutcheon. Anterior end with approximate-ly eight well-spaced, scaly radial ribs; central and poste-

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Explanation of Figures 55 to 70

- Figures 55–70. Diagramatic sketches of the inside of left valves of the species discussed here.
- Figure 55. Petricola (Petricola) botula; based on Skoglund Collection; Tizate, Nayarit, Mexico; length, 15.0 mm.
- Figure 56. P. (P.) carditoides; CAS 102524; Monterey, California; length, 32.7 mm.
- Figure 57. P. (P.) linguafelis; LACM 70-9; Salinas, Guayas Province, Ecuador; length, 4.2 mm.
- Figure 58. P. (P.) lucasana; CAS 102518; Puerto Peñasco, Sonora, Mexico; length, 22.3 mm.
- Figure 59. P. (Petricolirus) californiensis; Socorro, Baja California [Norte], Mexico; length, 28.3 mm.
- Figure 60. P. (P.) concinna; LACM 71.50.1; Bahía Bartolomé, Isla Bartolomé, Islas Galápagos; length, 20.3 mm.
- Figure 61. P. (P.) dactylus; SBMNH 133419; Punta Arenas, Magallanes Province, Chile; length, 25.6 mm.
- Figure 62. P. (P.) denticulata; CAS 024296; Canoa, Manabi Province, Ecuador; length, 33.5 mm.
- Figure 63. P. (P.) rugosa; ANSP 323775; Lurin, Lima Province, Peru; length, 24.8 mm.
- Figure 64. P. exarata; CAS 102591; Altata, Sinaloa, Mexico; length, 13.5 mm.
- Figure 65. P. hertzana; CAS 106035; paratype.
- Figure 66. P. olssoni; ANSP 252061; Peninsula Paracas, Ica Province, Peru; composite of two specimens; lengths, 12.3 mm and 15.0 mm.
- Figure 67. P. scotti; holotype; length, 16.9 mm.
- Figure 68. Choristodon robustum; SBMNH 143212; Bahía San Carlos, Sonora, Mexico; length, 21.8 mm.
- Figure 69. Petricolaria cognata; SBMNH 143213; Cochore, Guaymas, Sonora, Mexico; length, 43.7 mm.
- Figure 70. P. pholadiformis; CAS 102508; Woods Hole, Barnstable Co., Massachusetts; length, 39.8 mm.

rior slope with approximately 36 radial threads; dense commarinal threads also present. Pallial sinus of moderate depth, narrow, pointed anteriorly, paralleling but not confluent with pallial line; pallial line not bowed dorsally (Figure 70). Hinge teeth proportionately small, thin; right valve with a sharp, projecting anterior cardinal and a projecting, bifid posterior cardinal; left valve with a small anterior cardinal, a slightly bifid central cardinal, and a narrow posterior cardinal. Ligament shallow; nymph thin. Color white to light tan externally and internally. Length to 60 mm in eastern Pacific material [CAS 105782; Coyote Point, San Francisco Bay, California], to 71.3 mm in western Atlantic material [USNM 27089; Staten Island, New York].

Distribution and habitat: According to Carlton (1979: 514-517, 1992:495), this species was introduced, perhaps with Crassostrea virginica (Gmelin, 1791), in three localities in the northeastern Pacific: Willapa Bay, Pacific County, Washington (46.7°N), in about 1943 [LACM 17787, SBMNH 43253, CAS 105781, and many other lots; Kincaid, 1947]; San Francisco Bay, California (approx. 37.7°N), in about 1927 [SBMNH 17377, CAS 105782, and many other lots]; Upper Newport Bay, California (33.6°N), in about 1972 (V. L. Human, in Carlton, 1979:515), but not now surviving there (R. Seapy, e-mail, 28 January 1996). A lot in the CAS labeled Monterey, California [CAS 105783], is thought to represent a labeling error (Carlton, 1979:516). It does not seem to have spread beyond Willapa and San Francisco bays, where it occurs from the intertidal zone to 10 m, burrowing in clay, mud or other soft substrata. It is not common and populations are very patchy (J. T. Carlton, e-mail, 16 April 1996; A. Cohen, e-mail, 16 April 1996). I have examined 32 eastern Pacific lots.

In its native habitat in the western Atlantic, it occurs from Prince Edward Island, Canada [USNM 27105], to the Gulf of Mexico (R. T. Abbott & Morris, 1995:74). It was also introduced into the eastern Atlantic in 1890, and it now occurs from Norway to the Black Sea (Tebble, 1966:126). There are several papers that track the expansion of this species in the eastern Atlantic: Cooper (1896), Boettger (1907a, b), Schouteden (1907), Sikes (1910), Grahle (1932), Schlesch (1932), Rustad (1955). Records from west Africa and the southern Caribbean are based on other taxa (see Discussion under the previous species).

Discussion: Lamarck (1818) described *Petricola pholadiformis* from an unknown locality. Four years later, Say (1822) redescribed this species as *P. fornicata* from the western Atlantic. Conrad (1832) was the first to recognize that they were the same thing. Two years later, Conrad (1834) also indentified some specimens of this species as *P. dactylus*, but eventually Dall (1925) was able to conclude that the name of this South American species had been misapplied, and he proposed the name *P. pholadiformis lata* for such specimens. Gastranella tumida Verrill, 1872, was based on juvenile specimens, as first deduced by Dall (1900c:1061).

Campbell (1993) synonymized the eastern North American Pliocene *P. carolinensis* Conrad, 1863, and (probably) Pleistocene *P. rogersi* McGavock, 1944, with this species.

Petricolaria pholadiformis differs from *P. cognata* in having a broader, less produced posterior end; flat rather than curved scales on its radial ribs; heavier commarginal sculpture; and a narrower, more pointed pallial sinus. It differs from *Petricola dactylus* in being more elongate, thinner, having scales on its radial ribs, having more delicate hinge teeth, and in having a longer, narrower pallial sinus.

There are many accounts on the anatomy and biology of this species. The following are the most important of these: *Anatomy & Morphology*—Russell, in Gould (1841: 64–65), Perkins (1869:149), Gould (1870:92), Rice (1897:36, 66–67), Morse (1919:179–180), White (1942: 73), Purchon (1955), Taylor et al. (1973:275, table 15); *Reproduction & Development*—Coe (1943:182–183), Sullivan (1948:22–23, pl. 13), Loosanoff & Davis (1963: 115–117), Brousseau (1981); *Ecology*—Connell (1955), Burton (1958); *Burrowing*—Duvall (1963), Ansell & Nair (1969:862–863), Ansell (1970).

Excluded Taxa

Petricola amygdalina G. B. Sowerby I, 1834:47, was described without illustration from the Islas Galápagos, Ecuador. It was said to have been found in pteriid valves at 3-6 fms. [6-11 m]. By 1854, G. B. Sowerby II (1854b: 777) could not identify it, and no type material has been located at BM(NH). The original specimen, which measured 33 mm in length, 20 mm in height, and 12.7 mm in thickness, was described as being thin, subhyaline, yellowish, and with commarginal lamellae. Both Pilsbry & Vanatta (1902:551) and Bernard (1983:57) revived the Galápagos record of this species, the latter allocating it the subgenus Petricolaria. No museum specimens that might have been the basis of these records has come to light (Yves Finet, in correspondence, 23 January 1996), although the Galápagos specimen of the very different looking P. concinna [LACM 71-50.1] may account for Bernard's report. This species is best regarded as a nomen dubium and/or extralimital.

Choristodon cancellarus Verrill, 1885:435–436, described on the basis of a single, eroded left valve (USNM 44839) measuring 7.7 mm in length dredged off Chesapeake Bay in 70 fms. [128 m], has never been recollected. First figured by Verrill & Bush (1898:778. 896, pl. 96, fig. 2), it is probably not a petricolid because the sculpture is very even and the hinge has a broad dorsal area that lacks teeth (Coan, 1996:122, fig. 20). It may be from an offshore fossil deposit.

Petricola cordieri Deshayes, 1839:358, 1840:pl. 18, is

a long-recognized synonym of *Irusella lamellifera* (Conrad, 1837) (for example, Lamy, 1923b:322).

Petricola discors G. B. Sowerby I, 1834:46, was described from Lambayque, Lambayque Province, Perú $(6.7^{\circ}S)$, was said to have been obtained from hard clay. No illustration was ever published, and type material has not been located in BM(NH). The original specimen measured 20.3 mm in length, 14.0 mm in height, and 7.6 mm in thickness. An argument might be advanced that this is what is here known as *P. olssoni:* the locality, shape, brownish color, and the presence of only radial sculpture fit this species. On the other hand, the described smooth posterior end and clay habitat do not. Little point would be served by salvaging this taxon, for which a neotype would be required to achieve stability, and it is best regarded as a *nomen dubium*.

Petricola elliptica G. B. Sowerby I, 1834:46, is the original combination for the venerid *Irus (Paphonotia) elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Venerupis foliacea Deshayes, 1853:192–193, is a synonym of *Irus (Paphonotia) elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182). This species was listed as a *Rupellaria* by Carpenter (1857b:299, 1864b:668 [1872:154]) and by Tryon (1884:174, 435).

Venus lamellifera Conrad, 1837:251, is the original combination for the venerid *Irusella lamellifera* (Conrad, 1837). It was listed as a *Rupellaria* by Carpenter (1857a: 214, 1857b:299, 349, 1864b:536, 539, 540, 641 [1872: 22, 25, 26, 127]) and also as a *Petricola* (Carpenter, 1857b:229).

Ungulina luticola Valenciennes, 1846:pl. 24, figs. 5, 5a, b, was described on the basis of four specimens that are now conserved in the MNHN. It was been regarded as a synonym of *Petricola carditoides* (Conrad, 1837) (Dall, 1900c:1155; Bernard, 1983:57). However, the originally figured specimen, here designated **lectotype** (Figure 54), is instead paired valves of *Thracia curta* Conrad, 1837; it measures 10.4 mm in length, 9.1 mm in height, and 8.4 mm in thickness (this species was discussed by Coan, 1990:33–35). The paralectotypes are: 16.9 mm in length [*Petricola carditoides*], 12.8 mm in length [*Thracia curta*], and 7.0 mm in length [*Sphenia luticola* (Valenciennes, 1846), a different species described in the same work under the generic name *Corbula*].

Petricola oblonga G. B. Sowerby I, 1834:46, is a synonym of *Irus (Paphonotia) elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Venerupis paupercula Deshayes, 1854:5, described in error from New Zealand, has been synonymized with *Irus* (*Paphonotia*) *elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182). It was listed by Carpenter (1857b:299) as a *Rupellaria*.

Petricola solida G. B. Sowerby I, 1834:46, is a synonym of *Irus (Paphonotia) elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Petricola solidula G. B. Sowerby II, 1854a:770, is a

synonym of *Irus (Paphonotia) elliptica* (G. B. Sowerby I, 1834) (Keen, 1971:182).

Petricola subglobosa G. B. Sowerby I, 1823:fig. 6, was described without a known locality, with only an internal view of the valves provided. No original material is present in BM(NH). Carpenter (1864b:559 [1872:45]) associated the species with some of the synonyms of *P. car-ditoides*, perhaps because the ribs were described by Sowerby as being "decussatis." It is now best regarded as a *nomen dubium*.

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